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Morphological comparisons of brown frogs (genus *Rana*) from Sakhalin, Hokkaido and Primorsk

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One species of brown frog from Sakhalin, previously assigned to *Rana temporaria*, *R. chensinensis* or *R. semiplicata*, is very similar to *R. pirica* from Hokkaido in body coloration and skin texture. However, results of morphometric analyses indicate its intermediate nature between *R. pirica* and *R. dybowskii* from Primorsk. Clarification of the taxonomic status of this frog needs further study from different approaches.

INTRODUCTION

Two species of brown frogs (*Rana temporaria* group of BOULENGER, 1920) occur on Sakhalin island (BANNIKOV et al., 1977). One is unambiguously identified as *Rana amurensis* (BANNIKOV et al., 1977; KUZMIN et al., 1988), but the taxonomic status of the other is at present uncertain. It is usually regarded as *Rana chensinensis* (ORLOVA et al., 1977; KUZMIN et al., 1988) or sometimes as *Rana semiplicata* (BANNIKOV et al., 1977). However, recent taxonomic studies revealed that the Asian brown frogs that have long been collectively treated as *Rana chensinensis* actually include several distinct taxa (for review, see MATSUI, 1991 and MATSUI et al., 1993). As a result, the population of "*Rana*

Source : MNHN, Paris

chensinensis" from Hokkaido (KAWAMURA, 1962) was described as *Rana pirica* (MATSUI, 1991).

In describing *Rana pirica*, the senior author (MATSUI, 1991) restricted the range of this species to Hokkaido, but the close taxonomic relationship of the frogs on Sakhalin and Hokkaido has long been accepted (OKADA, 1930, 1931, 1966; NAKAMURA & UÉNO, 1963, 1965), and their taxonomic relationships await clarification. As a part of our studies to determine the taxonomic status of the brown frog from Sakhalin, we compared this population morphometrically with *Rana pirica* from Hokkaido and *R. dybowskii* from Primorsk.

MATERIALS AND METHODS

We examined a total of 71 preserved specimens of *Rana pirica* from Hokkaido (40 males and 31 females), 37 specimens of *Rana* sp. from Sakhalin (31 males and 6 females; fig. 1) and 20 specimens of *Rana dybowskii* from Primorsk (15 males and 5 females) (Appendix I). Seventeen body measurements were taken (Table I), mostly following MATSUI (1984). Briefly, they are: (1) snout-vent length (SVL); (2) head length (HL); (3) head width (HW); (4) snout length (SL); (5) snout height (SH = height of snout, measured at the level of the anterior corner of the eye, including the lower jaw); (6) intercanthal distance (ICD); (7) eye length (EL); (8) tympanum diameter (TD = greatest diameter); (9) internarial distance (IND); (10) interorbital distance (IOD); (11) upper eyelid width (UEW); (12) lower arm length (LAL); (13) hindlimb length (HLL); (14) thigh length (THIGH); (15) tibia length (TL); (16) foot length (FL); (17) inner metatarsal tubercle length (IMTL). All measurements were made to the nearest 0.1 mm with dial calipers. For morphometric comparisons, only sexually mature adults were used, and males and females were analyzed separately.

In order to examine interspecific and intersexual variation in each character dimension, analysis-of-covariance (ANCOVA) procedure was performed using SVL as the covariate. All measurements were log-transformed in this procedure. Each character dimension was then converted to a percentage ratio to SVL for further comparisons. For these ratio variables and frequency data for degree of toe webbing and position of tibio-tarsal articulation, Kruskal-Wallis tests with nonparametric multiple comparisons, Wilcoxon rank sum tests, or Mann-Whitney's U-tests were performed to detect the presence or absence of differences in the frequency distributions. The significance level was set at 0.05.

Programs designed and implemented by the S.A.S. (1989) package were used in the multivariate analyses. The analyses were performed through the facilities of the Data Processing Center, Kyoto University. A canonical discriminant analysis, performed by the CANDISC procedure was conducted and canonical variate scores of individuals were plotted on their respective axes. Further, a discriminant analysis (DISCRIM) was used to assess the degree with which each individual specimen was correctly classified into its home group.

Source : MNHN, Paris

Table I. - SVL ($\bar{x} \pm 1$ SE, followed by ranges in parentheses, in mm) and percentage ratios of each character dimension to SVL (medians, followed by ranges in parentheses) in brown frogs. See text for abbreviations.

	Males			Females		
	R. pirica (n = 40)	*Rana* sp. from Sakhalin (n = 31)	*R. dybowskii* (n = 15)	*R. pirica* (n = 31)	*Rana* sp. from Sakhalin (n = 6)	*R. dybowskii* (n = 5)
SVL	53.6 ± 0.7 (44.1-62.9)	54.6 ± 0.8 (39.7-60.8)	56.1 ±1.2 (50.9-67.4)	62.6 ± 0.9 (50.7-74.2)	62.8 ± 2.2 (56.3-71.4)	68.5 ± 1.9 (64.6-74.2)
HL/SVL	33.4 (31.1-35.7)	33.4 (31.1-35.8)	33.3 (31.5-35.7)	32.6 (30.0-37.1)	31.5 (25.6-33.2)	31.7 (30.0-34.2)
HW/SVL	32.1 (29.9-35.7)	33.7 (31.7-35.6)	34.1 (29.8-36.8)	32.3 (29.4-35.8)	33.3 (28.2-33.8)	32.6 (30.6-33.4)
SL/SVL	13.3 (11.5-14.4)	13.5 (11.9-14.9)	13.7 (12.9-15.3)	12.4 (10.7-13.3)	12.8 (12.4-13.4)	13.3 (12.6-14.7)
SH/SVL	9.8 (8.5-11.2)	9.6 (8.3-11.0)	9.5 (8.7-11.5)	10.3 (8.7-11.8)	10.1 (8.7-10.8)	9.8 (9.3-10.2)
ICD/SVL	12.8 (11.1-14.0)	12.2 (10.7-13.8)	11.9 (10.4-13.1)	11.8 (8.9-13.6)	12.0 (11.0-12.4)	11.4 (10.9-12.9)
EL/SVL	9.9 (8.2-11.7)	10.0 (8.6-10.8)	9.9 (9.4-11.3)	8.5 (7.7-9.7)	9.4 (8.3-9.8)	8.8 (8.7-10.6)
TD/SVL	6.5 (5.5-8.7)	6.7 (5.5-7.8)	7.0 (6.1-8.3)	6.2 (4.9-7.3)	6.4 (6.3-6.7)	6.9 (6.0-7.4)
IND/SVL	7.5 (6.3-8.6)	7.7 (6.9-8.3)	7.0 (6.3-7.5)	7.2 (6.1-8.5)	7.2 (6.7-7.8)	6.6 (6.3-7.3)
IOD/SVL	7.0 (6.4-8.1)	6.6 (5.2-8.1)	6.8 (6.2-7.5)	6.4 (4.8-8.0)	6.2 (6.2-6.7)	6.6 (6.5-7.4)
UEW/SVL	7.6 (6.6-9.4)	8.3 (7.2-9.5)	7.5 (6.7-8.3)	7.1 (5.8-8.8)	8.0 (7.6-8.8)	7.2 (7.0-8.2)
LAL/SVL	48.6 (44.1-52.7)	48.9 (46.7-53.1)	47.0 (44.0-50.8)	46.3 (41.9-49.8)	45.1 (43.8-46.1)	42.1 (40.6-44.7)
HLL/SVL	172.3 (161.9-181.9)	172.6 (160.0-186.2)	179.1 (165.2-191.3)	157.9 (141.0-170.2)	161.0 (155.0-163.1)	169.6 (159.9-172.4)
THIGH/SVL	48.5 (45.5-51.9)	48.9 (45.9-52.1)	50.2 (45.3-54.9)	46.7 (42.0-50.0)	46.2 (45.4-46.8)	47.7 (45.7-49.9)
TL/SVL	50.9 (47.8-54.6)	51.5 (48.7-54.4)	53.7 (49.8-59.1)	47.9 (42.0-52.2)	47.6 (46.9-48.8)	51.8 (48.9-54.3)
FL/SVL	57.0 (51.5-61.2)	58.3 (53.7-63.2)	60.5 (56.3-67.0)	51.6 (45.9-55.9)	53.1 (51.7-55.6)	54.1 (52.6-57.0)
IMTL/SVL	5.6 (4.7-7.0)	6.0 (5.0-7.1)	5.8 (4.3-6.7)	5.1 (3.9-5.9)	5.8 (5.6-6.2)	5.8 (5.3-6.6)

Source : MNHN, Paris

Table II. - Variation in the point reached by the tibio-tarsal joint when the hindlimb is bent forwards along the body in brown frogs. Figures indicate the number of specimens (percentage frequency in parentheses).

	Position of joint			
Species and sex	Tip of snout or forward	Anterior edge of eye to snout	Posterior to anterior edge of eye	Posterior edge of eye or behind
Males				
R. pirica	0	8 (20.0 %)	32 (80.0 %)	0
Sakhalin	1 (3.2 %)	6 (19.4 %)	24 (77.4 %)	0
R. dybowskii	0	11 (73.3 %)	4 (26.7 %)	0
Females				
R. pirica	0	0	22 (71.0 %)	9 (29.0 %)
Sakhalin	0	0	4 (100 %)	0
R. dybowskii	0	4 (80.0%)	1 (20.0 %)	0

Results

General characteristics of *Rana* sp. from Sakhalin

Morphometric data for *Rana* sp. from Sakhalin are summarized in Table I together with those for the other two species. Females of *Rana* sp. from Sakhalin are significantly larger in SVL ($\bar{x} \pm 1$ SE = 62.8 $\pm$ 2.2 mm) than males ($\bar{x} \pm 1$ SE = 54.6 $\pm$ 0.8 mm; t-test, $p < 0.001$). Lengths relative to SVL of EL, HL, SL, TD, IND, LAL, HLL, THIGH, TL, and FL were significantly greater in males (Mann-Whitney's U-test, two-tailed, $p < 0.05$). Nearly half of these characters are those of hindlimbs. Thus, when the hindlimb was bent forward along the body, the tibio-tarsal joint reached the point beyond the anterior edge of eye in about one-fourth of the males, but the joint at most reached the anterior edge of eye in females (Table II), though a significant statistical difference was not detected between the sexes (Wilcoxon rank sum test, two-tailed, $p > 0.05$).

Also, males of *Rana* sp. from Sakhalin tended to have slightly more developed toe webbing than females (Table III), but, probably due to the small sample size of females, significant sexual difference was detected only in the inner web of the second toe (Wilcoxon rank sum test, two-tailed, $p < 0.05$).

General comparisons of *Rana* sp. from Sakhalin with the other species

In general appearance, the *Rana* sp. from Sakhalin (fig. 1) more resembled *Rana pirica* than *Rana dybowskii*. *Rana* sp. from Sakhalin shared with *R. pirica* the following characteristics that were different from *R. dybowskii*: thick dorsolateral fold; occasionally

Source : MNHN, Paris

Table III. - Variation in the degree of toe webbing in brown frogs, expressed by the phalanges free of broad web. Figures indicate the number of specimens. in: inner web; out: outer web. Bold characters indicate the position of median.

Position of toe	Phalanx	*Rana* sp. from Sakhalin		*R. pirica*		*R.dybowskii*	
		Males	Females	Males	Females	Males	Females
1 out	0.5	4	0	11	0	2	0
	1	**27**	**6**	**25**	**28**	**13**	**4**
	1.5	0	0	4	3	0	0
2 in	1	0	0	1	0	0	0
	1.5	**20**	1	10	1	5	2
	2	11	**5**	**26**	**29**	**10**	2
	2.5	0	0	3	1	0	0
2 out	0.5	**16**	1	16	6	**12**	**3**
	1	15	**5**	**22**	**25**	3	1
	1.5	0	0	2	0	0	0
3 in	1.5	2	0	0	0	0	0
	2	**27**	**5**	19	15	**13**	2
	2.5	2	1	**21**	**16**	2	2
3 out	0.5	13	1	4	0	2	0
	1	**18**	**5**	**35**	**29**	**13**	**3**
	1.5	0	0	1	2	0	1
4 in	1.5	1	0	0	0	0	0
	2	**21**	3	7	4	**11**	1
	2.5	8	3	**31**	**25**	4	**3**
	3	1	0	2	1	0	0
4 out	1	3	0	2	0	1	0
	1.5	**18**	3	5	2	**9**	1
	2	10	3	**32**	**22**	5	**3**
	2.5	0	0	1	6	0	0
5 in	0	2	0	0	0	0	0
	0.5	**23**	**4**	**22**	12	**12**	**4**
	1	5	2	18	**17**	3	0
	1.5	0	0	0	1	0	0

Source : MNHN, Paris

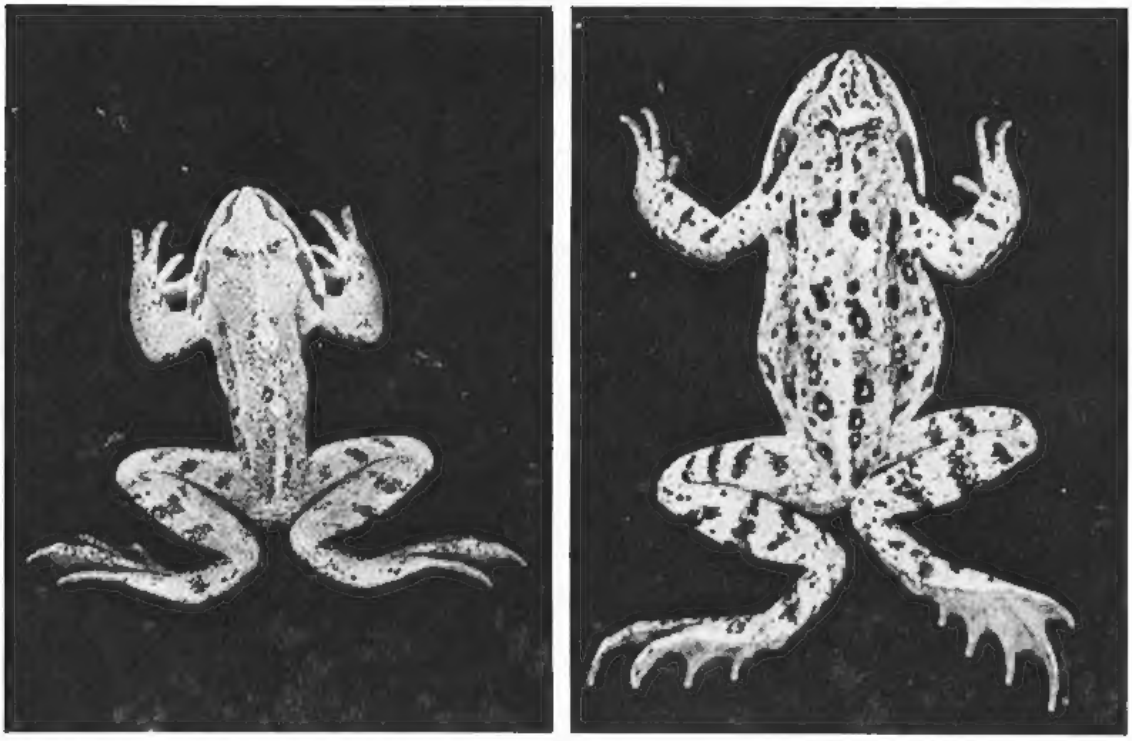

Fig. 1. – Dorsal view of a male (left: KUHE 11623, SVL = 58.1 mm) and a female (right: KUHE 11649, SVL = 71.4 mm) of *Rana* sp. from Sakhalin, Russia.

presence of partial, light stripe on middorsal line; usually presence of heavy dark markings covering the abdomen; dorsal skin with a few tubercles; ventral skin rugose; usually presence of a few dark spots on flanks.

In *R. dybowskii*, in contrast, the dorsolateral fold is usually thin; the light stripe on middorsal line is rarely present; dark markings on abdomen are absent or limited, even if present; the dorsal skin is nearly smooth; the ventral skin is smooth; dark spots on flanks are usually absent.

The degree of development of the outer metatarsal tubercle varied within each species, but the tubercle was less frequently present in *Rana* sp. from Sakhalin than in *R. pirica* or *R. dybowskii*. In *Rana* sp. from Sakhalin, the outer metatarsal tubercle was present only in 25 % of the specimens examined, whereas in both *R. pirica* and *R. dybowskii*, about 70 % of the specimens possessed the tubercle.

In males, *Rana* sp. from Sakhalin did not differ from *R. pirica*, but both of them are significantly different (nonparametric multiple comparison test, $Q_{cal} > Q_{0.05,\ 3} = 2.39$) from *R. dybowskii* in the position of the tibio-tarsal joint (Table II). Females showed a similar tendency, but the difference was not significant. On the contrary, *Rana* sp. from Sakhalin more closely resembled *R. dybowskii* than *R. pirica* in the degree of toe webbing (Table III). In males, *Rana* sp. from Sakhalin had more developed webbing than *R. pirica* in the inner webs of the second, third, and fourth toes and outer webs of the third and

Source : MNHN, Paris

fourth toes, but from *R. dybowskii* it differed only in the inner web of the second toe. In females, significant difference was found only in the outer web of the fourth toe between *Rana* sp. from Sakhalin and *R. pirica*.

UNIVARIATE COMPARISONS

Results of ANCOVA showed that all characters, except for IOD in *Rana* sp. from Sakhalin and IMTL in *R. dybowskii*, had significant correlations with SVL in males. On the contrary, many characters (HL, SH, EL, IND, IOD, UEW, LAL, HLL and FL in *Rana* sp. from Sakhalin, HL, HW, SL, ICD, EL, TD, IND, IOD, LAL, HLL, THIGH, TL, FL and IMTL in *R. dybowskii*, and UEW in *R. pirica*) showed insignificant correlations with SVL in females, probably due to the small sample size and small variation range in each sample. Significant deviation of the slope (α) from 1 (isomorphic relationship: MATSUI, 1984) in the regression line was observed in some cases. In males, SL, IND, LAL, THIGH and TL (fig. 2) in *Rana* sp. from Sakhalin, HL, HW, EL, IOD and LAL in *R. pirica*, and HW and LAL in *R. dybowskii*, were all bradymorphic ($\alpha < 1$) to SVL. On the other hand, HL, SL, SH, EL, UEW, HLL, THIGH and TL in *R. pirica* and SH in *R. dybowskii* were bradymorphic to SVL, but UEW in *R. dybowskii* was tachymorphic ($\alpha > 1$) to SVL in females. All the other regression lines significantly correlated to SVL were insignificantly different from 1 in coefficient of the slope.

Among the three species, differences in the slope of regression lines were found only in EL and THIGH in males. In EL, the slope in *R. dybowskii* was steeper than that of *Rana* sp. from Sakhalin, which in turn was steeper than the slope of *R. pirica*. On the other hand, the slope of THIGH in *R. pirica* was steeper than that of *R. dybowskii*, which in turn was steeper than that of *Rana* sp. from Sakhalin. By contrast, much more numerous differences were found among the three species in the position of the regression lines. In males, HW, SL, ICD, IND, IOD, UEW, HLL, THIGH, TL, FL and IMTL were found to differ in some combinations among the three species. Similarly, the position of the regression lines for HL, SL, EL, UEW, HLL, TL and IMTL differed in females, but, as noted above, these characters insignificantly correlated to SVL in one or two of the three species.

In this way, the results of ANCOVA were rather complex, and particularly in females, neither significant correlation of regression lines nor deviation from 1 in regression lines were observed in many cases. Therefore, the relative sizes of morphometric characters were simply expressed by percentage ratios to SVL. As a result, many characters showed significant differences ($Q_{cal} > Q_{0.05,\ 3} = 2.39$) among the three species.

Rana sp. from Sakhalin differed from *R. pirica* in seven of 16 characters compared: two characters in both sexes, four in males, and one in females. In both sexes, *Rana* sp. from Sakhalin had larger relative values in UEW (males: $Q = 4.04$; females: $Q = 2.95$) and IMTL (males: $Q = 2.93$; females: $Q = 3.35$) than *R. pirica*. Males of *Rana* sp. from Sakhalin had larger relative HW ($Q = 4.08$) and FL ($Q = 2.99$), and smaller ICD ($Q = 2.49$) and IOD ($Q = 3.89$) than *R. pirica*. Females did not differ in these characters, but *Rana* sp. from Sakhalin had larger EL ($Q = 2.45$) than *R. pirica*.

Source : MNHN, Paris

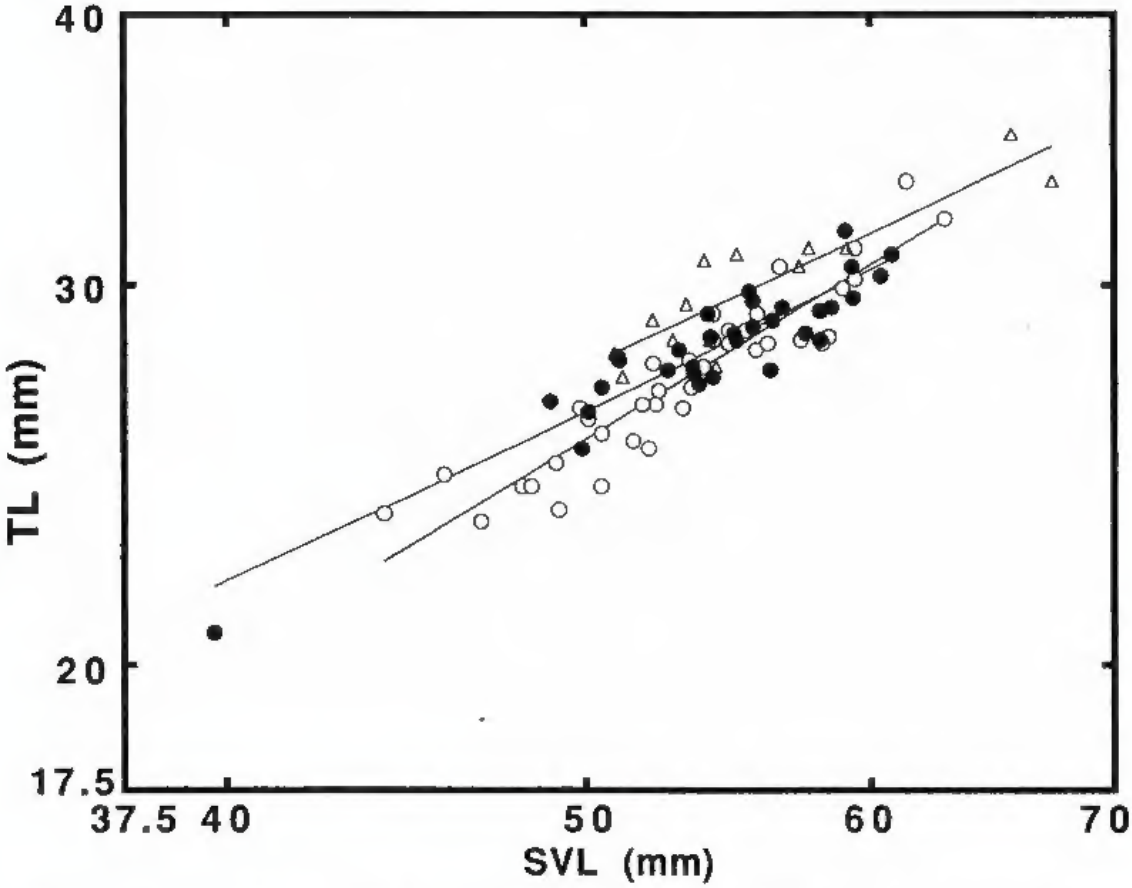

Fig. 2. – Allomorphic relationships between SVL and tibia length (TL) in males of *Rana* sp. from Sakhalin (closed circles: regression equation, log TL = 0.850 log SVL −0.027, r = 0.931), *R. pirica* (open circles: log TL = 1.010 log SVL − 0.310, r = 0.927) and *R. dybowskii* (open triangles: log TL = 0.768 log SVL + 0.135, r = 0.894).

In five (one character in both sexes and four in males) out of 16 characters compared, *Rana* sp. from Sakhalin differed from *R. dybowskii*. Both sexes of *Rana* sp. from Sakhalin had smaller value in TL (males: Q = 3.08; females: Q = 2.51). Also, males of *Rana* sp. from Sakhalin had larger IND (Q = 4.23) and UEW (Q = 3.36), and smaller HLL (Q = 2.43) and THIGH (Q = 2.66) than male *R. dybowskii* (fig. 3), but females did not differ in these characters.

The difference between *R. pirica* and *R. dybowskii* was the greatest and they differed in 11 out of 16 characters compared: four characters in both sexes, five in males, and two in females. In both sexes, *R. pirica* was smaller in TL (males: Q = 4.25; females: Q = 2.94), HLL (males: Q = 3.27; females: Q = 3.01), FL (males: Q = 4.28; females: Q = 2.51) and SL (males: Q = 2.45; females: Q = 2.74) than *R. dybowskii*. In males, *R. pirica* was larger in IND (males: Q = 3.92) and ICD (Q = 3.31), but was smaller in THIGH (Q = 2.44), HW (Q = 4.11), and TD (Q = 2.93) than *R. dybowskii*, while in females, *R. pirica* was larger in LAL (Q = 3.11) and smaller in IMTL (Q = 2.90) than *R. dybowskii*.

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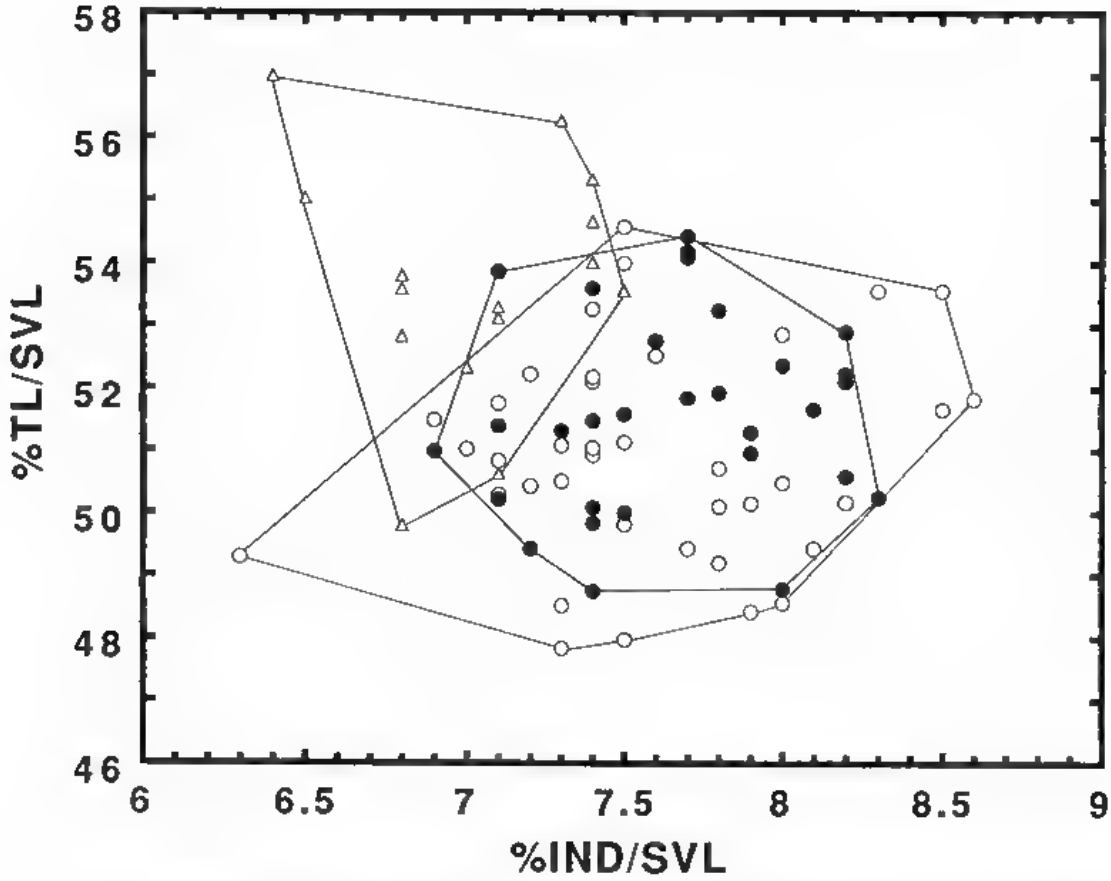

Fig. 3. — Relationships between relative tibia length to relative internarial distance in male samples of *Rana* sp. from Sakhalin (closed circles), *R. pirica* (open circles) and *R. dybowskii* (open triangles).

Thus, *Rana* sp. from Sakhalin is characterized by having a relatively wide upper eyelid and large inner metatarsal tubercle compared with *R. pirica*, and relatively short tibia compared with *R. dybowskii*. In general, these results of univariate analyses, as in those obtained from multivariate analyses, indicated an almost equally great morphological differentiation of *Rana* sp. from Sakhalin from both *R. pirica* and *R. dybowskii*, but the degree of differentiation is small compared with the greater difference between the latter two species.

MULTIVARIATE COMPARISONS

Results from the CANDISC are presented in fig. 4. In both sexes, all F values from the four criteria, e. g , Wilks' Lambda, Pillai's Trace, Hotelling-Lawley Trace, and Roy's Greatest Root Statistics, were significant at $p < 0.0001$, indicating significant geographical effect. In males, the eigenvalue of the first and second axes accounted for 3.453 and 1.379, respectively, and the first canonical variable accounted for 71.5 % of the total amount of

Source MNHN, Paris

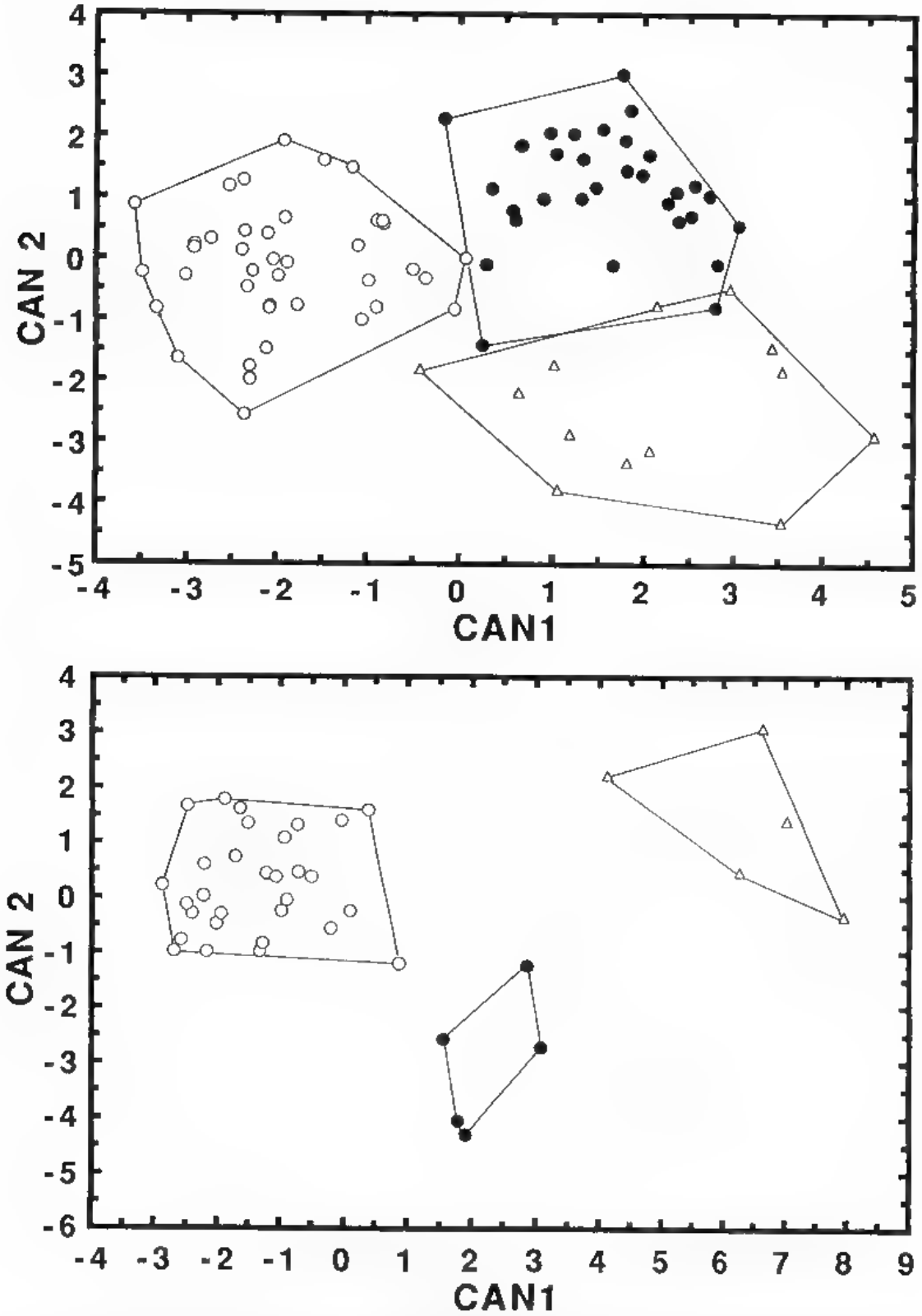

Fig 4. – Plot of first against second canonical variates for samples of *Rana* sp. from Sakhalin (closed circles), *R. pirica* (open circles) and *R. dybowskii* (open triangles). Top, males; bottom, females.

Source MNHN, Paris

Table IV. - Classification matrix based on linear discriminant function analysis in brown frogs. Entries along the main diagonal are "correct" matches of individuals to their source population.

Actual group	N	Predicted group membership		
		Rana sp. from Sakhalin	*R. pirica*	*R.dybowskii*
Males				
Sakhalin	31	26 (83.9 %)	2 (6.5 %)	3 (9.7 %)
R. pirica	40	3 (7.5 %)	36 (90.0 %)	1 (2.5 %)
R. dybowskii	13	2 (15.4 %)	1 (7.7 %)	10 (76.9 %)
Females				
Sakhalin	5	4 (80.0 %)	0 (0 %)	1 (20.0 %)
R. pirica	31	2 (6.5 %)	28 (90.3 %)	1 (3.2 %)
R. dybowskii	5	1 (20.0 %)	1 (20.0 %)	3 (60.0 %)

eigenvalues, whereas in females, the eigenvalue was 7.629 and 1.461, respectively, and the first variable accounted for 83.9 % of the total amount.

The absolute magnitudes of the standardized canonical discriminant coefficients are proportional to the relative importance of each character in separating the three species along each of the two canonical discriminant axes. In males, FL was the greatest contributor to separation on the first axis (2.766), followed by TL (2.764) and HLL (-2.651). On the second axis, LAL (1.220), HLL (-1.060) and IND (0.888) were the high contributors. Similarly, variables with high contribution on the first and second axes in females were LAL (-2.068), HLL (1.228) and TL (0.996), and TL (1.969), HL (-1.566) and HW (-0.930), respectively.

In males, *Rana* sp. from Sakhalin was nearly completely distinguishable from *R. pirica*, but completely overlapped *R. dybowskii* on the first canonical axis, while this situation reversed on the second canonical axis. Thus, on the first two axes, *Rana* sp. from Sakhalin was nearly completely distinguishable from *R. pirica*, and only slightly overlapped *R. dybowskii*. In this way, the intermediate position of *Rana* sp. from Sakhalin between *R. pirica* and *R. dybowskii* was clear in males. Separation was better in females, and the three species did not overlap on these axes.

Reflecting the similarities of the three species in gross appearance, the DISCRIM succeeded in assigning only 85.7 % (72 of 84) in males and 85 4 % (35 of 41) in females of the individual specimens to correct home population (Table IV). In males, the DISCRIM correctly classified 83.9 % (26 of 31) of *Rana* sp. from Sakhalin, with 9.7 % (3 of 31) of other specimens classified as members of *R. dybowskii*, and 6.5 % (2 of 31) as *R. pirica*. On the other hand, in females, four of five (80.0 %) individuals of *Rana* sp. from Sakhalin were correctly classified and all the remaining specimens were classified as members of *R. dybowskii* with only a low posterior probability (48.1%).

Source MNHN, Paris

Discussion

Rana sp. from Sakhalin was first recorded from the southern part of the island in 1870 by Dobrotvorsky and was identified as *R temporaria*. Since then, the brown frog from Sakhalin, together with that from Hokkaido (= *R. pirica*), have long been considered to be conspecific with this European species (Boulenger, 1886; Stejneger, 1907; Nikolsky, 1905, 1918; Okada & Kawano, 1923; Okada, 1930, 1931; Terent'ev & Chernov, 1949) However, it is now generally accepted that *R. temporaria* has 2 n = 26 chromosomes (Witschi et al , 1958) and its range does not extend to the Asian regions (Frost, 1985). By contrast, *Rana* sp. from Sakhalin is inferred to have 2 n = 24 chromosomes, like Chinese *R. chensinensis* and its allies including *R. pirica* (Seto, 1965; Green, 1983; Wei et al , 1990)

More recently, *Rana* sp. from Sakhalin and *R pirica* have often been regarded as populations of *R. chensinensis* (Kawamura, 1962; Okada, 1966, as a subspecies of *R. temporaria*; Orlova et al., 1977, Frost, 1985; Kuzmin et al., 1988), *R. dybowskii* (Nakamura & Uéno, 1963, as a subspecies of *R temporaria*; Nakamura & Uéno, 1965, as a subspecies of *R. chensinensis*) or *R. semiplicata* (Bannikov et al., 1977) Of these, *R. chensinensis* was described from the Qinling Mountains of China (David, 1875), which are geographically quite distant from Sakhalin or Hokkaido. On the other hand, *R. dybowskii* was described from near Vladivostok, Russia (Günther, 1876). From this pattern of distribution, the relationships of brown frogs from Sakhalin and Hokkaido were expected to be closer to *R. dybowskii* than to *R. chensinensis*, and recent studies of the Hokkaido population led to the description of *R. pirica* (Matsui, 1991), leaving the taxonomic status of *Rana* sp. from Sakhalin undetermined.

Taxonomic status of *R. semiplicata* is little understood The species was described by Nikolsky (1918) from two specimens possibly from Poltavka, Maritime Territory, and it was said to resemble *R tsushimensis* and *R. amurensis*, both of which have 2 n = 26 chromosomes (Orlova et al , 1977). Terent'ev & Chernov (1949) claimed that inaccuracies were contained in the original description, but from the description and figures of a type specimen, this species is not related either to *R. tsushimensis* or to *R. amurensis*, but seems to be synonymous with *R. dybowskii* (Matsui, 1991). Bannikov et al. (1977) included the coastal region of Russia and Sakhalin within the distribution range of *R semiplicata*, while Orlova et al. (1977) synonymized this species with *R chensinensis*. Matsui (1991) suggested that "*R. semiplicata*" from Sakhalin (Bannikov et al., 1977) was possibly conspecific with *R. pirica*.

Previous morphometric comparisons of *R pirica* with *R. dybowskii*, *R. ornativentris*, and topotypic *R. chensinensis* (Matsui, 1991; Matsui et al., 1993) indicated the presence of great differentiation between *R. pirica* and *R. dybowskii*. However, the results of morphometric analyses shown above indicate that *Rana* sp. from Sakhalin is not completely identical to either *R pirica* or *R dybowskii*, but is morphometrically intermediate between them. This result contradicts the taxonomic treatments made by Bannikov et al. (1977) with regard the coastal and Sakhalin populations as conspecific, or the prediction made by Matsui (1991) to associate the Sakhalin population with *R. pirica*.

Source MNHN, Paris

As noted by MATSUI et al. (1993), morphological differentiation seems generally preceded by genetical differentiation among brown frogs of the *R. temporaria* group, and the presence of even a subtle morphological difference between any two local populations seems to suggest the possibility of their independent taxonomic status. Additional studies from various approaches, especially biochemical ones, are necessary to elucidate the taxonomic position of *Rana* sp. from Sakhalin, and such studies are now underway. On the other hand, *Rana* sp. from Sakhalin is distinct from *R. chensinensis* in the characteristic swelling of water in the oviduct during preservation, as are *R. dybowskii*, *R. pirica* and a population of *R. chensinensis* from northeastern China (the Hashima-frog) (MATSUI, 1991), and these forms seem to constitute a monophyletic group.

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Source: MNHN, Paris

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APPENDIX I
SPECIMENS EXAMINED

The samples are stored at the Graduate School of Human and Environmental Studies, Kyoto University (KUHE) and in Sen TAKENAKA private collection (ST).

Rana sp. (n = 37). Sakhalin, Russia: Uglegorsk (48°40'N, 133°54'E): KUHE 11613-11627, 11644-11649, 11657-11670, 11680, 14138.

Rana pirica (n = 71) – Hokkaido, Japan: (1) Nikappu-cho (42°22'N, 142°19'E) KUHE 13871, 13876-13883, 13889-13891, 13893-13901, (2) Rankoshi-cho (42°52'N, 140°36'E) KUHE 13825-13828, 13833-13834, 13836, 13840-13842, 13844, (3) Kamishihoro-cho (43°21'N, 143°12'E). KUHE 13141-13149, 13152-13154, 13156, 13158-13160, (4) Obihiro-shi (42°53'N, 143°11'E) KUHE 13745, 13747, 13750-13751, 13753-13755, 13758, 13760; (5) Tomakomai-shi (42°40'N, 141°36'E) KUHE 13845-13847, 13850-13852, 13854, 13857, 13859-13861, 13863-13866.

Rana dybowskii (n 20) – Primorsk, Russia: Lazo (43°21'N, 144°04'E): KUHE 11721-11732; ST 01-02, 06-07, 09, 14, 16, 18

Corresponding editor: Emilio BALLETTO.

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Source MNHN, Paris

Site tenacity, within and between summers, of *Rana arvalis* and *Rana temporaria*

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Adult moorfrogs *Rana arvalis* and common frogs *Rana temporaria* were marked, released and recaptured during five summers in a 50 × 50 m large moist meadow site. All capture sites were noted. The distribution of number of captures per frog and the distance between successive capture sites were analysed. It is concluded that most frogs that were captured at least twice in the area occupied a permanent home range there. However, there was probably some change of centre of activity over time. The size of these home ranges was about 150 m² for *R. arvalis* and 330 m² for *R. temporaria*. There was no difference between sexes, nor between large and small frogs. Some frogs captured only once, especially *R. arvalis*, were probably temporary visitors. Many frogs returned to the study area in successive years, usually to the same part of the study area where they had spent the previous year.

Introduction

In the old days, an animal ecologist marked animals. Hopefully the animal could be recaptured or observed and identified A massive effort of this type yielded all sorts of basic autecological information: estimates of individual growth rate, population densities and individual movements. The prime example is the marking program of Fitch (1958) at the University of Kansas. No mammal, reptile or amphibian was allowed to remain unmarked. I carried out a similar program for Swedish brown frogs (*Rana arvalis* and *Rana temporaria*) on a small scale (50 × 50 m). I have previously published compilations of growth rate (Loman, 1978) and population dynamics (Loman, 1984) emerging from this work. The compilation of movements was not published at that time but follows here.

This study is an analysis of *R. temporaria* and *R. arvalis* marked and recaptured in a restricted area during part of five summers. The results are analysed to provide evidence for the nature of the frogs' summer movements. In contrast to what had been possible if radio transmitters were used, details in the movement patterns cannot be tracked. The study aims at determining whether a restricted home range is used, at least for part of the summer, and at yielding an estimate of the size of any home range used. I will also give information of the between-year home range use of the frogs.

Source MNHN, Paris

Study area and methods

The study was conducted in a moist meadow habitat in southern Sweden (55°40′N, 13°30′E). The study site was a 50 × 50 m part of a meadow with a uniform vegetation consisting of a thick layer of grasses and herbs, about 40 to 80 cm high. Scattered *Salix* bushes also occurred The site was about 200 m from the closest possible breeding sites for the study species.

The study site was thoroughly searched during each summer from 1972 to 1976 The study periods were July 11 to October 7 1972 (26 searches), July 2 to October 7 1973 (30), July 8 to September 9 1974 (17), August 4 to October 6 1975 (25), and August 6 to August 30 1976 (13). Each search lasted for about one hour. I walked back and forth on fixed paths in order not to disturb the habitat more than necessarily. These paths were about 2 m apart. All frogs seen were captured if they were considered possible adults (*R. arvalis* at least 36 mm long and *R. temporaria* at least 46 mm long). Frogs of this size may breed in the following spring (Loman, 1978). Only frogs actually measured to these sizes were considered further Each frog was individually marked by toeclipping and the capture site noted to the closest 1 m coordinates. Wooden sticks were placed as a 10 m grid to facilitate positioning.

Distances and time intervals between captures were significantly non-normal for both species (Lilliefors test, Wilkinson, 1990· all cases $P < 0.001$). After log transformation, the distributions for the *R. temporaria* data were not significantly different from normal (Lilliefors test: times, $P = 0.141$; distances, $P = 0.401$). By this criterion, the moor frog data differed somewhat from normality (Lilliefors test: times, $P = 0.047$; distances, $P = 0.030$). Nonetheless, the transformed data were used for both species in the significance tests.

Results

Distribution of captures per frog — estimating the population's size

Most frogs were only captured once (fig. 1) and were thus potential transients. To evaluate how common these were, I need an estimate of the total number of frogs at risk of capture in the study area, pooled over all study years. I estimated the size of this "population" (the sum of the five study years' population sizes) by fitting a negative binomial distribution to the data (Caughley, 1975: 154) and this yielded a surprisingly good fit for the moor frog (Table I). Extrapolating the fitted distribution to the zero class (frogs available for capture but never captured) yielded values for the total population at risk of capture. These were 1270 (3.5 times the total number captured) for *R. arvalis* and 598 (1.9 times the total number captured) for *R. temporaria*.

Source MNHN, Paris

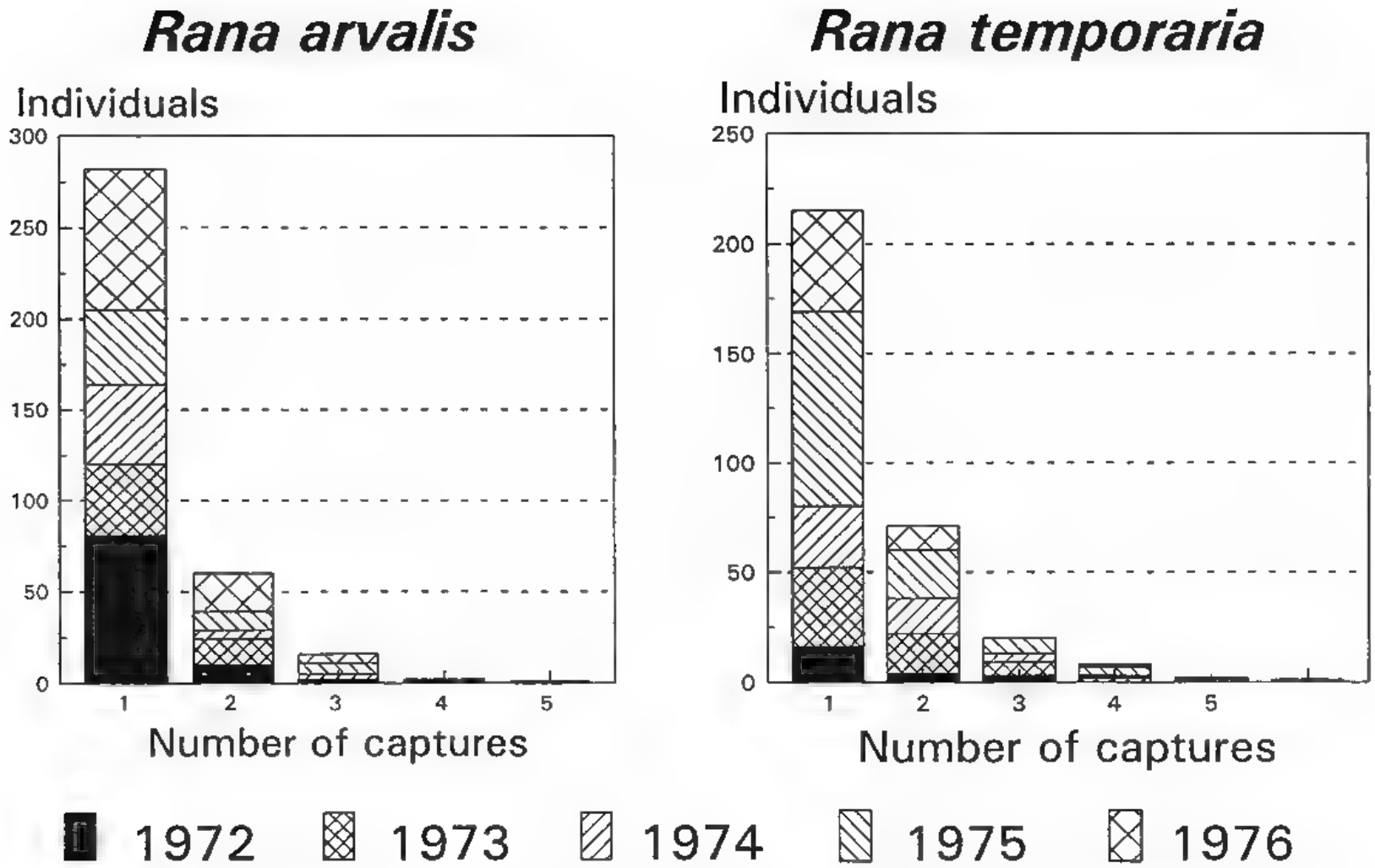

Fig. 1. — Distribution of number of captures per frog and year.

Source : MNHN, Paris

Table I. - Frequency distribution found and expected from a fitted negative binomial distribution. The classes of animals captured 4 times or more are pooled for the $\bar{x}$-tests.

	Rana arvalis		*Rana temporaria*	
Captures	Observed	Expected	Observed	Expected
1	282	286.5	215	254.3
2	60	63.0	71	82.9
3	16	13.8	20	26.1
4	2	3.0	8	8.1
5	1	0.7	2	2.5
6	0	0.1	1	0.8
7	0	0.0	0	0.2
$\bar{x}$	0.75		9.22	
d.f.	1		1	
P	>0.10		<0.01	

DISTANCE BETWEEN SUCCESSIVE CAPTURES

The average distance between two captures of an individual within a year was 6.10 m for *R. arvalis* and 9.45 m for *R. temporaria* (Table II). These distances are significantly different ($t = 2.89$, d.f. $= 171$ [pooled variances], $P < 0.001$) They are also both significantly different from the average distance of 100 random distances, 26.50 m (*R. arvalis* vs. random. $t = 14.2$, d.f. $= 176$ [pooled variances], $P < 0.001$; *R. temporaria* vs. random. $t = 10.7$, d.f. $= 193$ [pooled variances], $P < 0.001$). These random distances were formed as the distance between 100 pairs of rectangular distributed (in the interval 0 to 50) random coordinates.

Sex and size effects

There was no difference in the average distance between two captures, between the sexes, in any of the species (Tables II and III). There was no effect of size, which presumably would reflect age (LOMAN, 1978) (Table III).

Successive captures of individual frogs

First to second versus first to third capture

If a frog was recaptured more than once, the second recapture tended to be about as far from the original site as the first recapture (Table IV).

Time between captures

There was a slight tendency for capture sites based on captures far apart in time to be further apart than those separated by only a short time (fig 2). Based on all captures

Source MNHN, Paris

Table II. Distance between successive captures of one frog. For frogs captured more than twice, an individual mean value was used; a frog captured N times yielded N-1 values; distance between capture 1 and 2, between 2 and 3, etc. The table reports the average of these individual mean values.

	Mean	S.D.	N	Test for a sex difference	
				t	P
Rana arvalis					
Females	6.78	5.70	36	0.60	0.55
Males	5.74	4.14	39		
All	6.10	4.90	78		
Rana temporaria					
Females	9.80	9.89	33	0.73	0.47
Males	9.24	7.86	61		
All	9.45	8.53	95		
Random	26.50	13.15	100		

Table III. - Four way ANOVA, testing simultaneously for effects of year, sex, frog size, and time between capture and recapture on the distance between two captures.

Species	Source	d.f.	F	P
Rana arvalis	Year	4	0.27	0.89
	Sex	1	1.39	0.24
	Size	1	0.96	0.22
	Time int.	1	2.83	0.039
Rana temporaria	Year	4	0.92	0.46
	Sex	1	0.16	0.69
	Size	1	0.28	0.60
	Time int.	1	1.66	0.20

Source MNHN, Paris

Table IV. Distance between first and second versus distance between first and third capture of a frog. Values for frogs captured more than three times is based on a mean value for each frog. A frog captured N times yielded N-2 values. Only frogs captured at least three times are considered in this table. The test is a pair-wise t-test and the probabilities given are one-tailed.

		1st to 2nd site		1st to 3rd site		Test	
	N	Mean	S.D.	Mean	S.D.	t	P
Rana arvalis	17	7.63	5.23	7.13	6.85	0.15	0.44
Rana temporaria	29	8.30	5.89	9.83	7.31	1.46	0.075

(including several values for some frogs, recaptured more than once), this effect was significant for both species. When correcting for other factors, this increase in distance was only found to be significant for *R. arvalis* (Table III).

Time since marking for recaptured frogs

If marked frogs tended to leave the study area after some time, those frogs that were recaptured would be a biased sample of all frogs marked. They would mainly be those that had been marked (for the first time in that year) during the time shortly preceding the time of attempted recapture. The time they had been marked should be less than the "population mark age", i.e. the average time all frogs marked that year had carried their marks. Because successively more of those marked early would leave the study area, this tendency should increase with time passed since marking started in that season. However, there were no such tendencies (fig. 3).

Between-year recaptures

Return rate

Quite a large number of marked frogs were recaptured in the following year. Information of growth rate obtained during the present field work and previously published (Loman, 1978) was used to classify frogs as "large" or "small" adults. As large adults were, in each year, those classified that already in the previous year were adults (i.e. at least 36 and 46 mm respectively) and thus subject to capture and marking (if found) already in that year. Overall, 33 % (*R. arvalis*) and 47 % (*R. temporaria*) of all "large" adults found in one year had actually been captured and marked also in the preceding year (Table V) This is only moderately less than the proportion expected (42 % and 67 % respectively) if all frogs that were marked in one year and survived to the next also returned to the study area.

Source MNHN, Paris

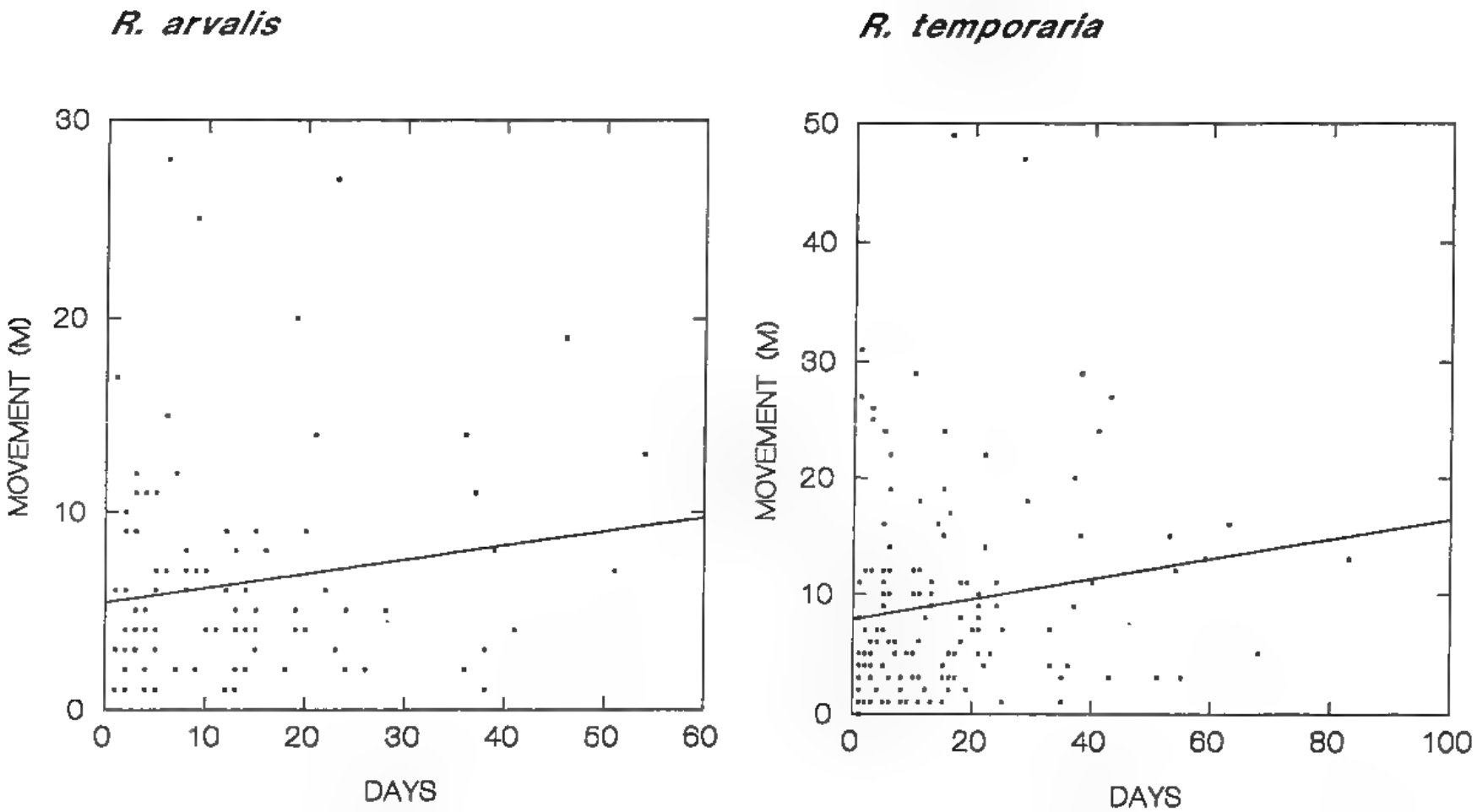

Fig. 2. – Relation of time between two captures and distance between the two sites. The correlation is significant for both species (*R. arvalis*: r = 0.23, d f. = 101, P = 0.010; *R. temporaria*: r = 0.16, d f = 137, P = 0 024). If the degree of freedom-values are reduced to the number of different frogs involved, the values are still significant (*R. arvalis*: d f = 78, P < 0 025, *R temporaria*: d.f. = 95, P < 0.05). All P-values are based on one-tailed tests.

Source : MNHN, Paris

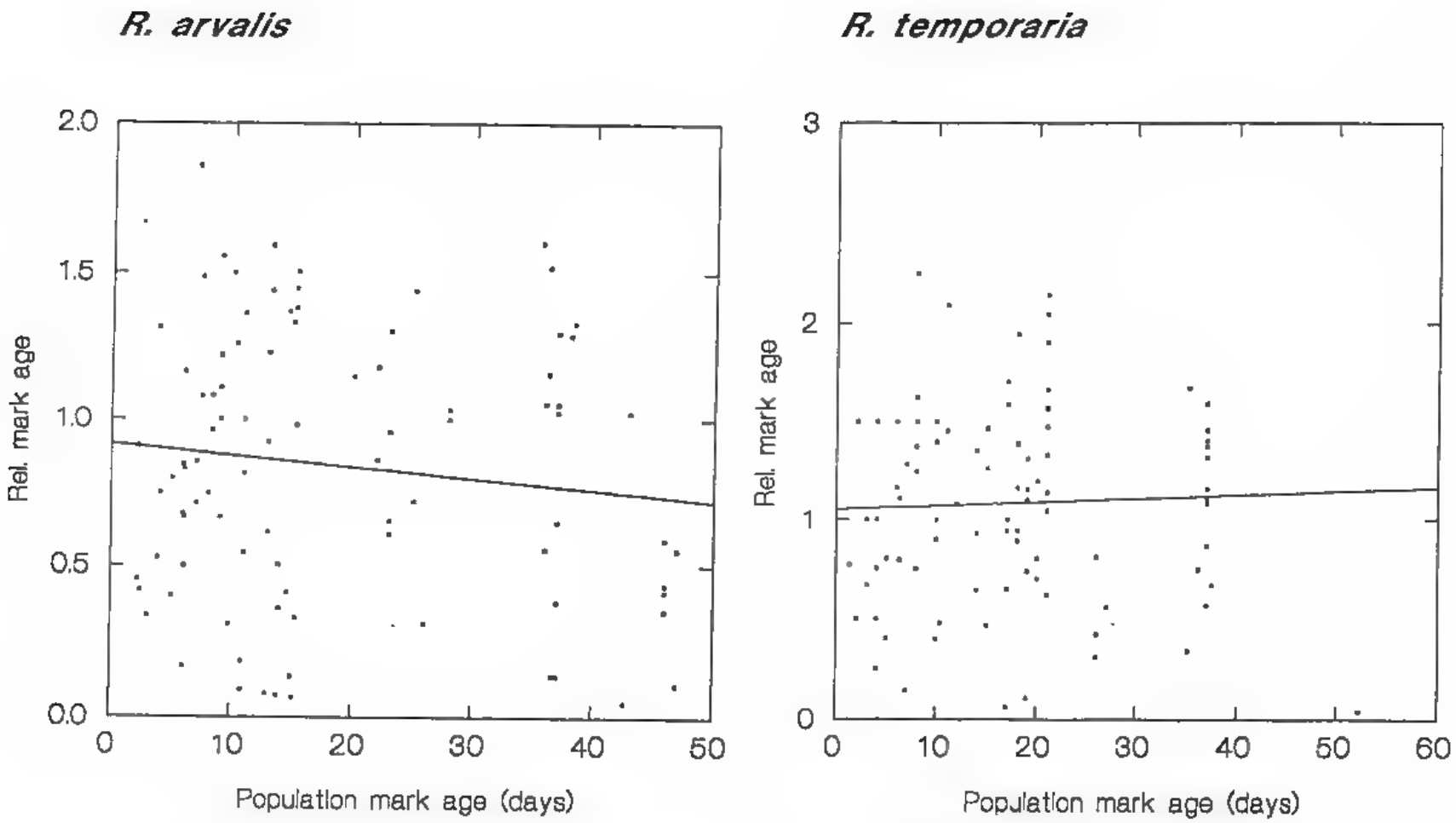

Fig. 3 — Relation between the "relative mark age" and the average time all frogs marked in that year had carried their marks ("population mark age"). "Relative mark age" is, for each capture, the time since the recaptured frog was first marked, divided by the "population mark age" on the day of that capture. There is a positive correlation for *R. temporaria* but it is far from significant ($r = 0.045$, d.f. = 105, $P = 0.65$). The slope for *R. arvalis* is negative, a direction that is excluded from being significant a priori (i.e. a one-tailed test).

Source : MNHN, Paris

Table V. - An analysis of the probability that a frog returns to the study area in successive years. "Captures T-1" is the number of frogs captured and marked in the study area in the year preceding T. "Population size T 1" is the estimated number of frogs in that year. Population size was estimated with the method of SCHUMACHER & ESCHMEYER (in SEBER, 1973: 139) (LOMAN, 1984). "Proportion marked in T-1" is the quotient between these. "Large adults T" is the number of frogs captured year T that were large enough to have been catchable in year T-1 (LOMAN, 1978). "Recaptures T" is the number of frogs captured in year T that were marked in the previous year. "Proportion recaptures T" is the quotient between the last two figures. There were too few captures of *R. temporaria* in 1973 and 1974 to warrant the computation of the last quotient.

Year T	Captures T-1	Population size T-1	Proportion marked T-1	Large adults T	Recaptures T	Proportion recaptured T
Rana arvalis						
1973	91	269	0.34	19	6	0.32
1974	48	54	0.89	13	6	0.46
1975	48	161	0.30	37	13	0.35
1976	56	96	0.58	38	10	0.26
Total	243	580	0.42	107	35	0.33
Rana temporaria						
1973	25	24	0.83	1	1	
1974	68	53	0.65	3	2	
1975	51	82	0.62	9	5	0.55
1976	129	249	0.52	14	6	0.43
Total	273	408	0.67	30	14	0.47

Between-year site tenacity

The frogs that returned to the study site and were recaptured in a second year were usually found close to the site where they had been found in the preceding year. The mean distance between the two sites was 6.5 m (S.D. = 6.37, N = 28) for *R. arvalis* and 12.8 m (S.D. = 9 64, N – 12) for *R. temporaria*. If there were several captures in one year of an individual, the arithmetic mean was used. These distances were not significantly different from the average distance between two capture sites in one year (Table II) (*R. arvalis*. t = 0.30, d.f. – 104, P > 0.10; *R. temporaria* t = 0 51, d f. – 105, P > 0.10).

Source MNHN, Paris

Discussion

Nature of home ranges

What was the nature of the summer movements of the frogs? The site tenacity was striking. Distance between any two captures of a frog was significantly shorter than that between two random points in the study area. This distance was found by simulation. Therefore it is obvious that at least most frogs that were recaptured did have a home range, in the sense of a "restricted area, more or less regularly used". The most extreme model for a summer home range would be a definite, small area, traversed throughout almost daily. Such a model is supported by the fact that the distance between capture sites 1 and 3 was not larger than that between 1 and 2. Thus, sequences of distances between three captures of a frog did not indicate any sort of directional movement.

However, there was a significant (but numerically rather slight, see the linear regressions in fig. 2) tendency for captures far apart in time to also be far apart in space. This can be interpreted as representing a gradual shift in home range location, or at least in centre of activity within home range, over time.

If frogs tended to stay in a home range for some time, but then move much further and at least leave the study area all together, this would "dilute" the marked population. At the beginning of the study period each year, all marked (but see below) frogs would be available for capture. The average time a recaptured frog had been marked would be similar to the average time since marking for all marked frogs in the population. However, later in the season, some of the frogs marked early would have left the study area and a disproportionate fraction of those recaptured would have been frogs that settled (and were marked for the first time) recently. The average time a recaptured frog had been marked would at this time tend to be less than the average time since marking for all frogs in the population. However, such a pattern was not discernible (fig. 3). This suggests that frogs with a home range in the study area at the beginning of each study season (July-August) tended to stay there at least until the end of this (up to September). However, if some frogs moved very quickly through the study area, only being available for capture once, they would not affect this pattern. They would be equally unavailable for capture at the beginning as at the end of the capture season.

On transients

Although the evidence is that most frogs captured at least twice were permanent residents in the study area, this cannot be shown for all those captured only once. These may have been unavailable for recapture because they were only temporarily present in the study area. The question can be somewhat elucidated by analysing the distribution of captures. It is appropriate to attempt fitting the distribution found to a negative binomial (see first section of *Results*) as this distribution results from situations with different capture probabilities for different individuals (Caughley, 1975). This was obviously the

Source MNHN, Paris

case because the effort differed between different years. The fit was very good for *R. arvalis*, so some confidence can be put in the expected number of individuals not captured at all in this species, more than three times the total number captured. This capture efficiency was surprisingly low. The individuals never captured are both those that remained resident in the study area without being captured and those that only briefly entered it (some of these latter could also contribute to the high number of frogs captured only once). It seems however improbable that all these should have remained for long in the study area without being captured. I judge a substantial number of those *R. arvalis* only captured once to be transients. The evidence is less conclusive for *R. temporaria* because the fit was poorer and because the estimated class of zero captures was smaller. Still, I would suggest also that some *R. temporaria* were transients to the study area. Apart from possible true nomads, these are frogs changing home range (though I have shown above that this is not a very common behaviour), or frogs that make temporary excursions from home ranges outside the study area. I have previously (LOMAN, 1981) shown that the presence of transient frogs is necessary to explain the pattern of recolonisation of an area where *R. temporaria* were removed DOLE (1965a) has shown that leopard frogs (*Rana pipiens*) make long excursions, outside their regular home ranges, during rainy nights. Such a phenomenon may explain the pattern found here.

An alternative explanation to the presence of transients would be high mortality. However, yearly mortality in the study population was previously calculated to 61 % (*R. arvalis*) and 36 % (*R temporaria*) which appears to be normal for terrestrial ranids (LOMAN, 1984). Also, I would expect most mortality to take place during the spring and autumn migration.

SIZE OF HOME RANGES

For both species, the data suggest that males and females as well as small and large individuals, had home ranges of similar size. What was the actual size of the home ranges? The small number of recaptures makes it impossible both to infer the shape of the home ranges and the individual variation. However, a rough impression can be gained from the following calculation. By means of simulations, the home range size that would give the same average distance between two random points (in the simulated home range) as the observed distance (Table II) between two capture sites can be calculated. These calculations were based on two alternative models for the nature of the home range With a rectangular distribution model I calculated the diameter of the home range periphery. This was 13.3 m for *R. arvalis* and 20.5 m for *R. temporaria* respectively. With a normal distribution model, I calculated the diameter of a circle encompassing 95 % of the activity. This was 15.5 m for *R. arvalis* and 24.0 m for *R. temporaria* respectively. Because we do not know the actual distribution of activity in the home range and there are several forms of sampling errors, the values calculated can only be considered a rough estimate of the magnitude of the home ranges One conclusion is that, at least for the *R. temporaria* which had the largest home ranges, most frogs had home ranges that overlapped the border of the study site. This should further tend to underestimate home range sizes. Also, it is

Source MNHN, Paris

obvious from the information of density in the study area (see first section of *Results* and LOMAN, 1984) that the home ranges of the studied frogs overlapped widely, both intra- and interspecifically.

BETWEEN-YEAR MOVEMENTS

Surprisingly many frogs returned to the study area in successive years. The proportion of all "large" adults that were already marked when captured for the first time in a year was almost as large as the proportion of all frogs estimated to have been marked in the study area in the previous year (see second section of *Results* and Table V). This calculation suggests that 79 % (0.33/0.42) of all *R. arvalis* and 70 % (0.47/0.67) of all *R temporaria* returned to the study site. These figures rely heavily on the estimations of population sizes. Because of biases and sampling errors in these estimates as well as sampling errors in the other figures, it is only possible to state that a substantial proportion, possibly almost all frogs alive, returned to the study site. Because of the arbitrary nature of "return" (here defined as return to a 50 × 50 m square), a more precise answer, even if it were possible to give, would only be of limited use However, the tendency for many frogs to return precisely to the same summer home range is clear; those that returned did actually do so to the part of the study area where they spent the previous summer.

COMPARISON WITH OTHER STUDIES

It is striking that few studies of this subject seem to have been published recently. The original list of references, compiled in 1981, contained quite a few comparable studies (Table VI). One of the few recent studies of amphibian summer home ranges is that by SINSCH (1988a). He employed a more sophisticated technique, trailing toads (*Bufo bufo*) with special devices, leaving a thin thread after the animal. That technique has previously also been used by DOLE (1965a), working with leopard frogs (*Rana pipiens*). However, it seems that everyone now expects studies of animal movements to employ radio transmitters. Though this certainly is justified, it emerges that little work, based on radio transmitters, has been published on frog movements. Studies that do are work by VAN GELDER and BUGTER (1987) on (one) *R. arvalis*, a report by FALLER-DOEPNER et al (1991) on the post-breeding migration of *R. temporaria*, a study of summer home ranges of *Bufo americanus* (WERNER, 1991) and another study by SINSCH (1988b) on breeding behaviour of *Bufo calamita*. It seems that the promise of radio transmitters has discouraged work employing conventional capture-recapture studies. Actually, it is probably only recently that transmitters small and long lived enough for useful work with frogs (but for the largest species) have been available. Future work with radio transmitters will yield more realistic descriptions of frog movements and home range use than is possible with capture-recapture methods, the results of which must be analysed to provide indirect evidence for the nature of the movements.

Nonetheless, most previous studies, like this one, have reported that frogs during the nonbreeding season tend to occupy restricted areas, home ranges. Examples include: *Rana*

Source MNHN, Paris

Table VI. - Published information on summer home range areas in frogs. Age categories are adult and subadult. If only mean distance between capture is given, this is found in the table, together with an estimate of home range area (made with the "rectangular model" above). DOLE (1965b) and KRAMER (1974) give direct estimates of home range area, computed with the minimum polygon method. Sizes of adult frogs are from CONANT (1958), STEBBINS (1966) and own data. ad: adult; sad: subadult. MD: Mean distance between captures (m)

	Age	Size (mm)	MD	Area (m²)	N	Reference
Rana pretiosa	ad, sad	50-100	12	(534)	23	CARPENTER, 1954
Bufo boreas	ad, sad	60-125	13	(627)	19	CARPENTER, 1954
Gastrophryne olivacea	ad	20-35	33	(4040)	52	FITCH, 1958
Acris crepitans	-	15-35	36	4810)	34	PYBURN, 1958
Bufo terrestris	-	40-75	13	(627)	27	BELLIS, 1959
Rana sylvatica	ad, sad	35-65	12	(534)	298	BELLIS, 1965
Rana arvalis	sad		12	(534)	16	HAAPANEN, 1970
Rana arvalis	ad	35-55	5	(93)	35	HAAPANEN, 1970
Rana temporaria	sad		8	(237)	96	HAAPANEN, 1970
Rana temporaria	ad	45-70	8	(237)	23	HAAPANEN, 1970
Bufo americanus	ad	28-50		21	5	WERNER, 1991
Bufo bufo	ad	50-70	4	(59)	29	HAAPANEN, 1974
Bufo bufo	sad		5	(93)	22	HAAPANEN, 1974
Pseudacris triseriata	ad	20-35		490	9	KRAMER, 1974
Rana pipiens, site I	ad	50-85		370	28	DOLE, 1965b
Rana pipiens, site I	sad			280	17	DOLE, 1965b
Rana pipiens, site II	ad	50-85		90	18	DOLE, 1965b
Rana pipiens, site I	sad			80	4	DOLE, 1965b
Rana arvalis	ad	36-55	6	(133)	78	This study
Rana temporaria	ad	46-70	9.5	(330)	95	This study

clamitans (MARTOF, 1953), *R. pretiosa* (CARPENTER, 1954; TURNER, 1960), *R. sylvatica* (BELLIS, 1965), *R. pipiens* (DOLE, 1965a-b), *R. arvalis* and *R. temporaria* (HAAPANEN, 1970), *Bufo boreas* (CARPENTER, 1954), *B. terrestris* (BELLIS, 1959), *B. bufo* (HEUSSER, 1968; HAAPANEN, 1974; SINSCH, 1988), and *B americanus* (WERNER, 1991); *Acris crepitans* (PYBURN, 1958); *Pseudacris triseriata* (KRAMER, 1974); and several tropical species (INGER, 1969). The home range areas reported are similar in size to those found by me (Table VI).

According to some authors, the home range may change during the course of one season: see BRECKENRIDGE & TESTER (1961) for *Bufo hemiophrys*, TURNER (1960) for *Rana pretiosa*, and WERNER (1991) for *Bufo americanus* I could not detect evidence of this This may mean that it was really of unusual occurrence in my populations. It could also be because my study only lasted for part of the summer seasons. Also, it may be a matter of how to interpret a pattern. Based on telemetry, VAN GELDER & BUGTER (1987) published

Source MNHN, Paris

a detailed, and very instructive, map of the movements of a *Rana arvalis* during two summer months The frog spent the full period within an area of about 20 × 30 m. During shorter periods it usually stayed within a more restricted area. However, it did also return to previous centres of activity, qualifying the whole area as a home range. This would probably correspond to the pattern I interpret from my data – essentially a restricted home range but with some change of activity centre over time. However, depending of the time scale used, it could also be characterized as changes of home range.

In their studies, MARTOF (1953), FITCH (1958), TURNER (1960), BELLIS (1965) and DOLE (1965b) found, as I did, a tendency for frogs to return to the same home range in successive years

I think my results provide a rough but useful picture of these two frog species' summer movements. However, we miss information on how and when the summer home range is established and also more detailed information on the use of space within the home range, including possible exploratory movements outside the "regular" home range. Also, it is not clear to what extent there are between-year shifts in home range and if such shifts are restricted to any particular age classes. Much of this work will undoubtedly benefit from the use of telemetry.

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Dispersal of *Rana temporaria* tadpoles in large fishponds

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Dispersal of *Rana temporaria* tadpoles was monitored from hatching to metamorphosis by systematic sampling at regularly distributed points of two large fishponds in the Jurassian Bresse (Eastern France). Dispersal showed two successive phases. During the first phase, shoals of tadpoles dispersed from the breeding site towards different directions. Then, the shoals spread out and the tadpoles colonized the shallower parts of the pond. They did not colonize the entire pond banks but only the shallower ends, i. e. the largest shallow areas occupied by a high density of vegetation. They emerged on the side of a pond that was the shadiest. Despite great differences in vegetation, mode and dynamics of tadpole dispersal did not differ between the two ponds.

INTRODUCTION

The question of tadpole dispersal is not very well documented. The literature has been mainly concerned with the diel pattern of distribution in small ponds (BEISWENGER, 1977, in *Bufo americanus*; GRIFFITHS, 1985, in *Rana temporaria*). The diel patterns observed in these two species are similar and may be summarized as follows: during the morning, the tadpoles migrate from the deepest zone of the pond towards the banks and aggregate in the shallow areas while temperature is increasing; at dusk, they return to the deepest parts of the pond. ANGELIER & ANGELIER (1968) noted aggregations of tadpoles of *Rana temporaria* on the banks during sunny days. As suggested by these observations, this diel cycle is probably thermo-dependent. Whereas water temperatures reach highest values along the bank during the day, during the night they are highest at the bottom. However, *R. temporaria* tadpoles may move from warmer to cooler water during dispersal (GRIFFITHS & MYLOTTE, 1986)

Tadpole social behaviour during the entire larval period has been described qualitatively in *R. temporaria* by SAVAGE (1961) and GUYÉTANT (1975). According to the latter, tadpoles are gregarious after hatching. They stay for one week at the spawning site where they feed on the gelatinous envelopes of the clutches They remain near the banks at less than 10 cm depth and disperse in the whole pond at the age of twelve to fifteen days, three months after hatching, they come back towards the banks and form aggregations

Source MNHN, Paris

before metamorphosis. According to SAVAGE (1961), *R. temporaria* tadpoles may remain gregarious for three to six weeks; they then disperse into several separate shoals, apparently based on food resources; eight to nine weeks after hatching they have a solitary life characterized by few feeding movements. These studies were carried out in small fishfree ponds

The surface of the pond and the diversity of its microhabitat probably influence tadpole dispersal. The previous observations concerned only small ponds where tadpoles may wander quickly throughout the pond Dispersal has not been described in large ponds such as fishponds with a surface of several hectares, which provide a higher diversity of microhabitats. Our purpose is to describe precisely the dispersal of tadpoles of *Rana temporaria* during the whole larval period and during froglet emergence in two large fishponds that attract a very large number of breeders (JOLY, 1991, AUGERI & JOLY, 1993) This monitoring was based on systematic sampling of tadpoles at points regularly distributed in the two fishponds.

MATERIAL AND METHODS

STUDY SITES

The two fishponds are located 9 km apart in Jurassian Bresse (Jura Department, between Lons-le-Saulnier and Dôle, altitude 200-215 m). Jurassian Bresse is a mosaic of deciduous forests (*Quercus, Fraxinus* and *Carpinus*), crops, meadows and fishponds devoted to carp farming. These ponds are dried every winter and filled again with rain or brook water. A 1.5 to 3 m deep central ditch leads to a draining point at the deepest end (3 m deep maximum) of each pond. The opposite bank has one or several shallow "tails". Average pond depth is about 0.7 m. Adult *Rana temporaria* usually breed in a tail. Daguin fishpond (3 ha) is surrounded by cultivated lands and meadows. Its tail is adjacent to a little wood. Thévenon fishpond (3.5 ha) is within a forest. Conductivity measured during the spawning period was 161 $\mu S.cm^{-1}$ at Daguin and 34.9 $\mu S.cm^{-1}$ at Thévenon. The higher value at Daguin is due to the proximity of field and pasture. The aquatic vegetation of each pond was mapped during June. Temperature values were regularly recorded at the same hour at several points of the two ponds at a depth of 0.5 m.

SAMPLING MODE

In 1989, *Rana temporaria* tadpoles were collected in the two ponds on five dates regularly distributed over time, from egg hatching to froglet metamorphosis (6 April, 19 April, 4 May, 22 May, 5 June). Samples along transverse transects were taken from a boat. The distance between two successive transects was about 30 m. Samples were uniformly distributed along each transect (about every 40 $\pm$ 5 m) Hence the number of samples per transect varied from five in the wider parts (one in the middle, two near the

Source MNHN, Paris

banks and two at intermediate points between the middle and the banks) to four and three (middle and banks) in the narrower parts. Sixty-six and seventy-seven points were visited at each date at Thévenon and at Daguin respectively. Three standardized sweeps of a 40 × 40 cm net (0.5 mm mesh) were made at each site from the bottom to the surface. Sampling was always carried out by the same operator. Depth was measured at each sampling point. From 5 to 9 June, we searched the edges of the two fishponds to determine where the froglets left the ponds. Maps of tadpole dispersion were computed using GraphMu on a Macintosh (THIOULOUSE, 1989).

RESULTS AND DISCUSSION

POND DESCRIPTION

The shallowest parts of the ponds (less than 1 m) showed two different shapes. Whereas they were narrow at the lateral banks, they widened out in the tails (fig. 1)

Thirtheen and sixteen macrophyte species were recorded at Thévenon and Daguin respectively (fig. 1). Six species were common to both ponds, *Carex riparia, Glyceria* sp., *Iris pseudacorus, Utricularia vulgaris, Scirpus lacustris* and *Sparganium erectum*. Floating species (*Trapa natans, Potamogeton lucens*) occupied large areas at Daguin but were scarce at Thévenon. The deepest part of Thévenon was covered by Characeae. This plant family was absent at Daguin. The banks were colonized by *Carex* sp. at Thévenon and by *Scirpus lacustris* at Daguin. The communities which occupied the pond tails were different: *Glyceria* sp. and *Carex* sp. were the most frequent at Thévenon, *Sparganium erectum, Phragmites australis* and *Typha angustifolia* were the most frequent at Daguin. Daguin is a more eutrophic pond than Thévenon. Vegetation richness at Daguin probably is a consequence of enrichment in mineral salts due to field drainage. Light levels were also higher at Daguin.

Mean temperature values were not significantly different between tails, lateral banks or central parts of the two ponds (two-ways ANOVA, see temperature values in Table I).

TADPOLE DISPERSION

Though beginning earlier at Daguin, tadpole dispersal presented some similarity between the two ponds (fig. 2) The dispersal process went through several phases. About one week after hatching, the tadpoles left the remains of the gelatinous mass. The first tadpoles which were found far from the spawning site were aggregated in some particular points (6 April at Daguin, 19 April at Thévenon). Their first movement was not a diffusion-like dispersal from the spawning site but rather appeared as a group movement of several thousand tadpoles, during about one week. In such shoals, physical contact between tadpoles was frequently observed. After this shoaling movement, tadpoles straggled more widely in the entire pond tails (19 April and 4 May at Daguin, 4 May at

Source MNHN, Paris

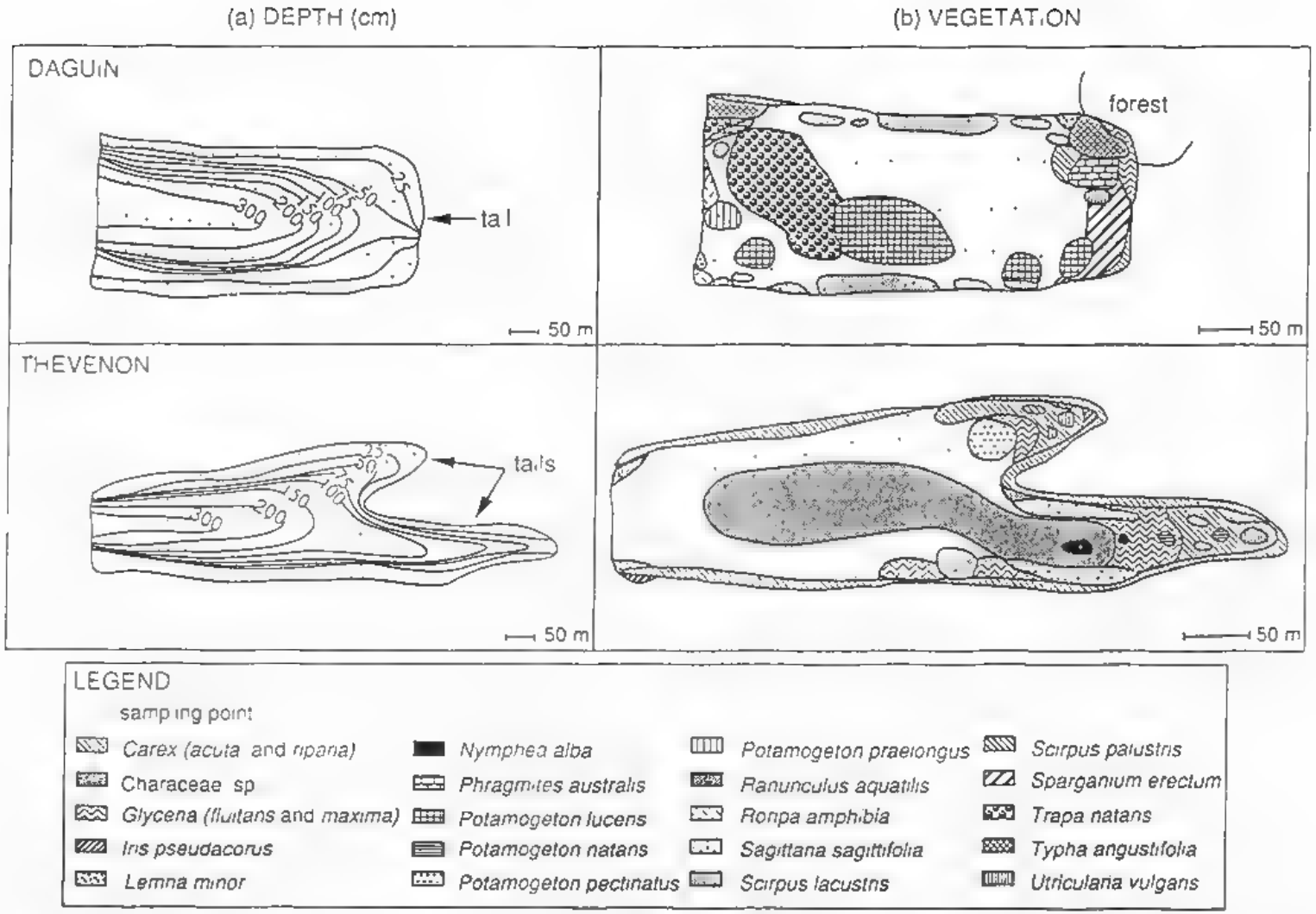

Fig. 1. – (a). Depth isolines in the two ponds the pond tails show a wide area of shallow water. (b) Maps of aquatic vegetation in the two ponds, Daguin and Thévenon. Twenty aquatic plant species have been noted in the two ponds, 16 in Daguin and 13 in Thévenon

Source : MNHN, Paris

Table I. – Temperature mean values (in °C) recorded at each date in the central parts, the lateral banks and the tails of the two ponds.

Dates	Daguin			Thévenon		
	Central parts	Lateral banks	Tails	Central parts	Lateral banks	Tails
6 April	8 6	9 2	9 6	9.2	9.6	10.1
19 April	8.9	9.5	10.1	9 5	9.8	11 0
4 May	12.4	13.6	14.2	14.2	14 8	16 0
22 May	14.5	15.3	16.0	15.5	16 3	17.2
5 June	15.3	16.7	18.2	17.7	18.4	19 5

Thévenon). Physical contact between tadpoles became less frequent. Finally, two months after hatching, they returned to the banks of the tails (22 May) where they emerged (5 June).

In our study, the habitat parameters considered as influencing tadpole distribution were depth, temperature and vegetation. It is clear that tadpoles did not colonize the entire pond but only its shallower parts (< 75 cm) (fig. 3) and did not colonize all the banks but only the ones situated in pond tails (fig. 2). They did not spread out further than 150 m from the spawning site. Previous studies have shown that tadpoles prefer both shallow water and high temperatures (NOLAND & ULTSCH, 1981; FLOYD, 1984; DUPRÉ & PETRANKA, 1985). Tadpole distribution observed in our study may be due to depth rather than to temperature which was on the average not significantly higher in the tails than in the central parts or in the lateral banks of each pond.

Shifts in vegetation occupation occurred during tadpole development in both ponds (fig. 4). At Daguin, at the beginning of April, the tadpoles reached highest densities in *Sparganium erectum*, *Scirpus lacustris* and *Phragmites australis* (6 April). The tadpoles then spread towards patches of *Potamogeton lucens*, *Glyceria* sp and *Utricularia vulgaris* (19 April; 4 May; 22 May). Before metamorphosis (5 June), they occupied only *Sparganium erectum* and *Glyceria* sp. patches. They did not colonize *Trapa natans*, *Potamogeton praelongus* or *Sagittaria sagittifolia*. At Thévenon, at the beginning of the development (6 April), they were found in zones of *Glyceria* sp. Then, whereas some tadpoles remained in *Glyceria* patches, a lot of them shifted (19 April) to patches of *Carex riparia*, *Utricularia vulgaris*, and, to a lesser extent, *Potamogeton pectinatus* and *Scirpus lacustris*. Before metamorphosis, they mainly occupied patches of *Glyceria* sp. and *Carex riparia* (4 June). They avoided Characeae (fig. 4). As a whole, tadpoles mainly inhabited species of shallow water but only those that occupy the tails. Contrarily to the lateral banks, tails constitute large areas of shallow water and of high density of vegetation

Source MNHN, Paris

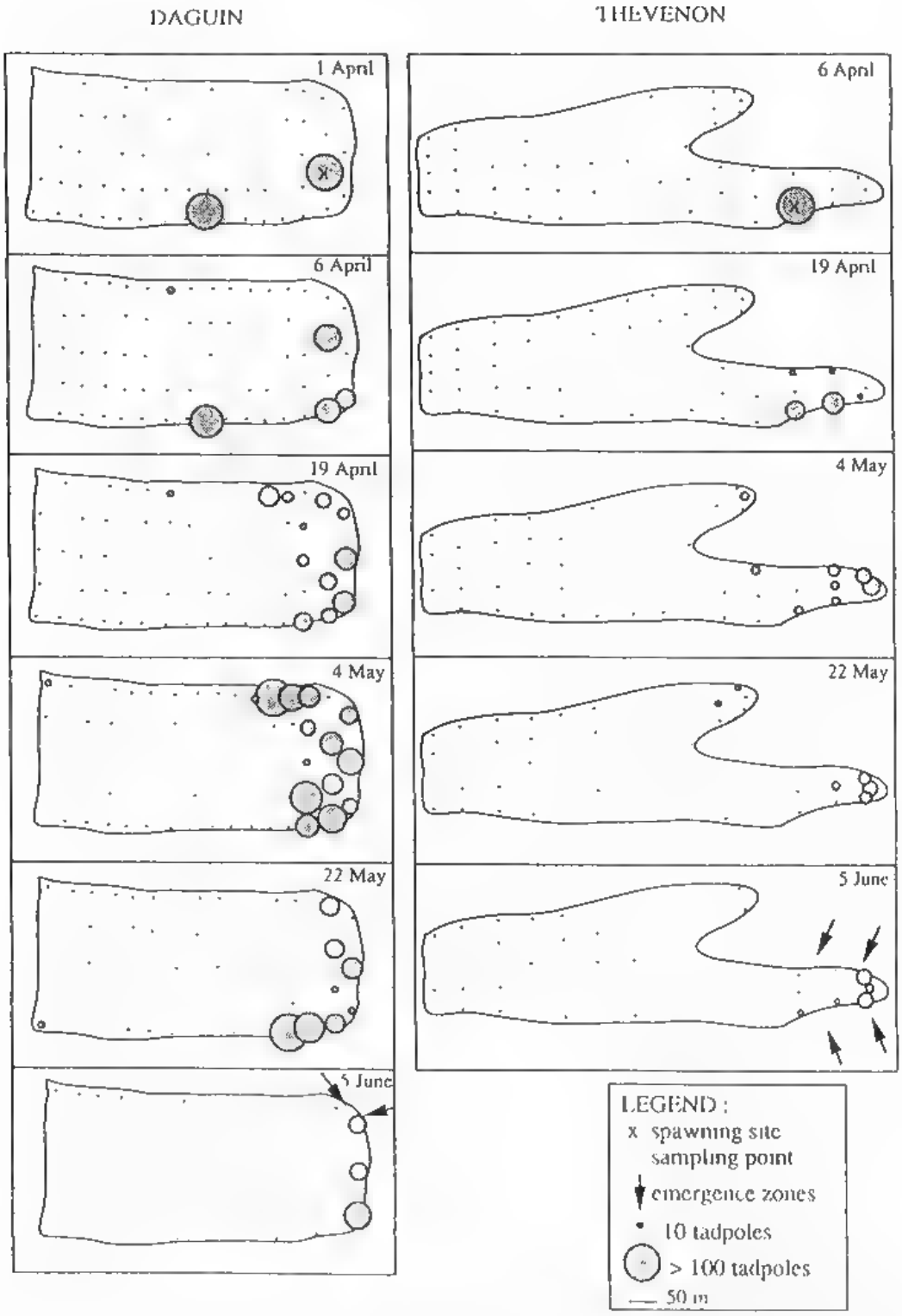

Fig 2 – Dispersion of tadpoles at each sampling date The size of each circle is proportional to the number of tadpoles collected according to a logarithmic scale The size of the circles shown in the legend are given as examples of tadpole numbers

Source MNHN, Paris

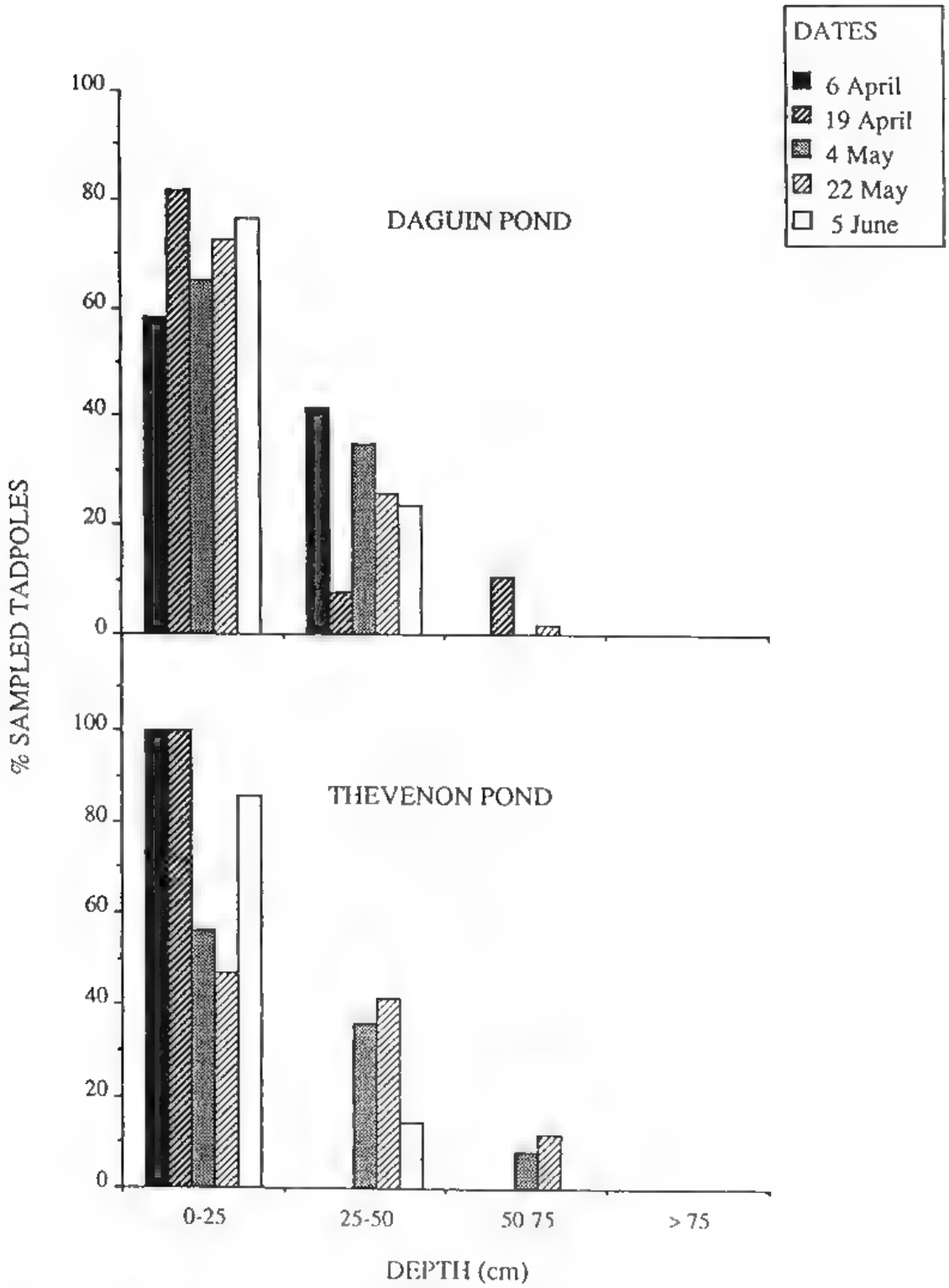

Fig 3. – Relationship between tadpole density (expressed in percentages) and water depth for the five sampling dates On the first date (6 April), tadpole dispersal has only begun in Daguin pond.

Source MNHN, Paris

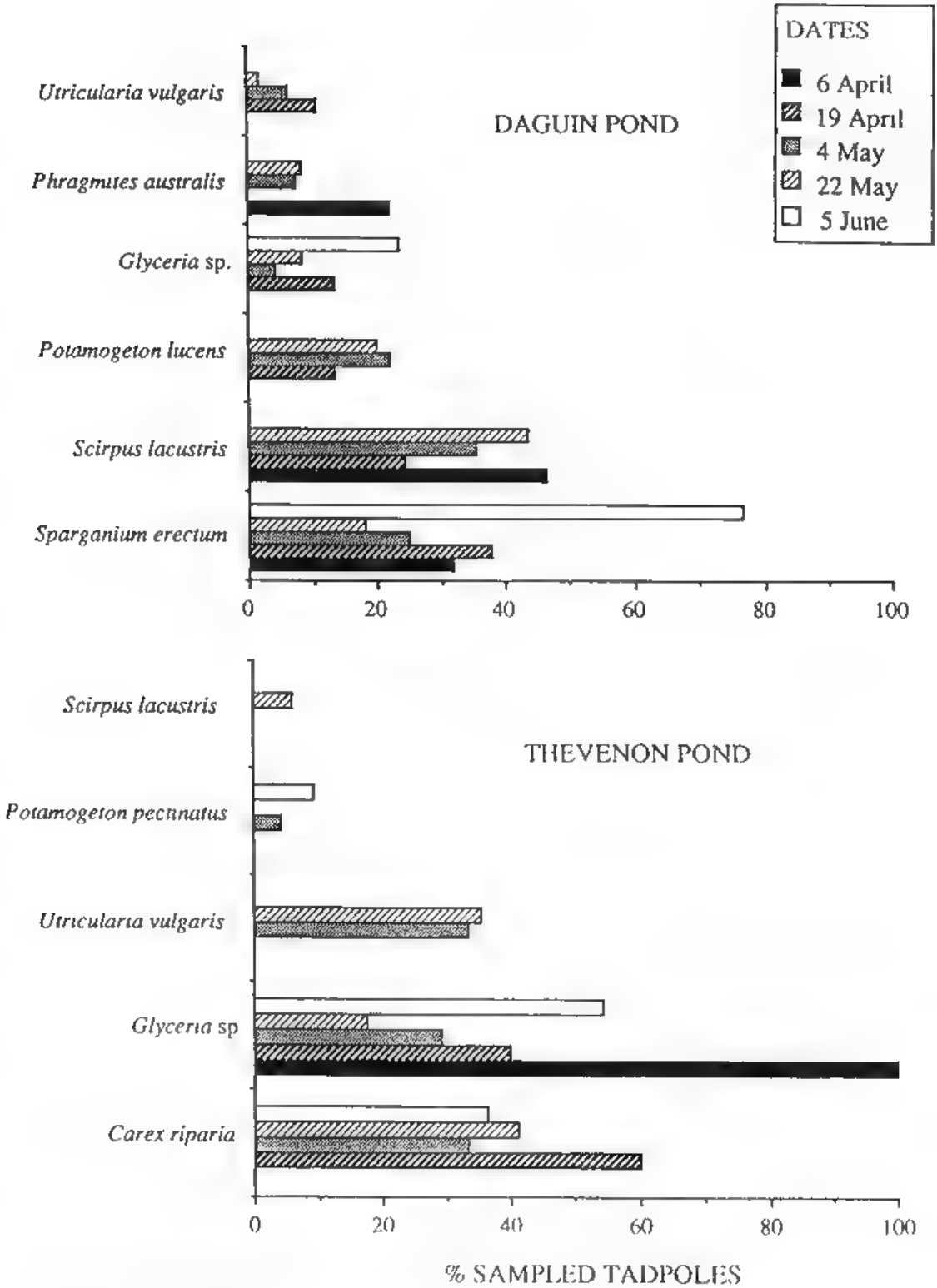

Fig. 4. Relationship between tadpole density (expressed in percentages) and plant species for the five sampling dates.

Source MNHN, Paris

Another factor, not measured in our study, which might influence tadpole dispersion, was the presence of fishes which reached rather high densities in the two ponds (personal observations). Indeed, as fishes are known to prey heavily on tadpoles (BEEBEE, 1983; KATS, PETRANKA & SIH, 1988), they may restrict tadpole dispersion to the parts of the ponds where vegetation provides a refuge against predation (CLAUSNITZER, 1983).

Metamorphosis also occurred in pond tails. The presence of vegetation and a gentle slope may help to prevent tadpoles from drowning, what has been observed during metamorphosis in *R. temporaria* (SAVAGE, 1961; ASHBY, 1969). At Thévenon, froglets emerged on both sides of each of the two pond tails toward the forest At Daguin, the froglets left the pond on the side of the little wood which is adjacent to the fishpond tail. Emigration in that direction may be due to an attraction of froglets by forest. In contrast to KOSKELA's (1973) observations, metamorphosis occurred in sunny weather; hence movement toward the forest may ensure favourable conditions for froglet life (ASHBY, 1969). According to SMIRINA (1980), froglet mortality is the highest during the first weeks after metamorphosis. The hypothesis of an attraction of froglets by forest has to be tested experimentally.

RÉSUMÉ

La dispersion des têtards de grenouilles rousses (*Rana temporaria*) a été suivie depuis l'éclosion jusqu'à l'émergence, par un échantillonnage systématique en des points régulièrement distribués, dans deux grands étangs de Bresse jurassienne (Est de la France). Cette dispersion comporte deux phases successives. Au cours de la première phase, des bancs de têtards se dispersent depuis le site de frai dans différentes directions Ensuite, ces bancs se diffusent et les têtards colonisent les parties les moins profondes de l'étang. Il est remarquable qu'ils ne colonisent pas entièrement les rives, mais seulement les zones de queue d'étangs, zones de faible profondeur les plus vastes comportant une forte densité de végétation. Ils émergent du côté le plus ombragé de l'étang. Malgré de fortes différences de végétation, le mode et la dynamique de dispersion des têtards ne diffèrent pas entre les deux étangs

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Age structure and survival rate in Alpine newts (*Triturus alpestris*) at high altitude

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Individual ages of 67 Alpine newts from a karst plateau in the Northeastern Calcareous Alps of Austria (Totes Gebirge, 1650 m altitude) have been assessed using skeletochronology of cross sections of the humerus. Both sexes start to reproduce at the age of 10 years, longevity exceeds 20 years and the oldest animal survived to an age of 22 years.

Survival rates estimated from age structure and mark-recapture experiments appeared lower in males, causing a female-biased sex ratio. Males may be subject to increased mortality during the spring migration.

INTRODUCTION

Skeletochronological studies of *Triturus* have shown that age at first reproduction is delayed and longevity increased with increasing altitude and latitude of the breeding site (DOLMEN, 1983; CAETANO et al., 1985; CAETANO, 1990; CAETANO & CASTANET, 1993). Decreased ambient temperatures lead to reduced metabolic rates, which in turn cause slower growth and delayed sexual maturity (JØRGENSEN, 1992). Age and survival in the Alpine newt were studied on the southwest plateau of the Totes Gebirge (1650 m), the largest karst massif (590 km^2) in the Northeastern Calcareous Alps of Austria. This massif generally receives more than 2200 mm precipitation annually and snow cover is present more than 196 days each year (DINÇER et al., 1972), breeding sites were covered with ice from the beginning of November until mid-June during the study period. Some of the breeding sites are former dolines, where temperatures are reduced by the settling of cold air.

MATERIAL AND METHODS

Alpine newts were collected from Lake Dreibrüdersee (1643 m) and from a pond (1650 m) situated approximately 1 km east from the lake in a neighbouring valley A mountain range with peaks up to 1950 m separates the two breeding sites. Lake

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Dreibrüdersee fills a former doline (137 m diameter) and is surrounded by steep rocky slopes.

Individual ages of 36 females and 8 males from Lake Dreibrüdersee, and 23 males from the nearby pond, were assessed by skeletochronology using cross sections of the humerus. Mean snout-vent lengths of breeding females and males in Lake Dreibrüdersee were 57.06 ± 0.22 mm (95 % C.L.) and 49.53 ± 0.32 mm respectively. Only males found dead were used for age determination. Live females were anaesthetized with MS 222 and the entire sample was fixed in 10 % formalin. Diaphysial regions of the humerus were decalcified with 40 % EDTA, dehydrated in Isopropylalcohol, stored over night in Methylbenzoat, and embedded in Paraplast. Cross sections 10 mm in thickness were stained with DELAFIELD-Hematoxylin (ROMEIS, 1968) for several hours and then destained with hydrochloric acid.

The mean survival rate (Φ) for the age classes 14 to 19+ in females from Lake Dreibrüdersee and 14 to 17 in males from the pond were calculated from the age structure by using the ROBSON & CHAPMAN formula (KREBS, 1989: 432-433):

$$\Phi = \frac{T}{\Sigma N + T - 1},$$

where:
Φ = average finite annual survival rate or probability of survival; finite survival rates can range from 0 to 1; a survival rate of 0.65 means that in average 65 % of the population survive from one year to the next;
N_x = number of individuals in age class x;
ΣN = number of all animals from age classes x to x+i: $N_x + N_{x+1} + N_{x+2} + \ldots + N_{x+i}$; for females from Lake Dreibrüdersee this is: $N_{14} + N_{15} + \ldots + N_{19+}$;
T = sum of the coded ages times their frequencies when coded age is found by setting the youngest included age class to 0, the next age to one and so forth: $0N_x + 1N_{x+1} + 2N_{x+2} + \ldots + iN_{x+i}$, for females from Lake Dreibrüdersee this is: $N_{15} + 2N_{16} + \ldots + 5N_{19+}$.

Animals from age classes 10 to 13 were omitted from the calculations because they were underrepresented in the sample (fig. 2).

This formula is only valid for a stationary population in which recruitment and survival are relatively constant. As these assumptions are hardly fulfilled in natural populations, the calculated values should be treated as rough estimates which allow comparison of average survival rates between sexes and between different populations.

Adults (855 females, 277 males) in Lake Dreibrüdersee were marked individually by tattooing with Alcian blue between 1986 and 1992 (JOLY & MIAUD, 1990) Population size and finite annual survival rates were estimated with a multiple mark-recapture census (JOLLY-SEBER method, KREBS, 1989: 37-43). In contrast to the ROBSON & CHAPMAN method this model does not assume a constant survival rate.

Reliability of population size estimates was assessed using less complex models (PETERSEN and SCHUHMACHER methods, KREBS, 1989: 16-36) which work only in a closed

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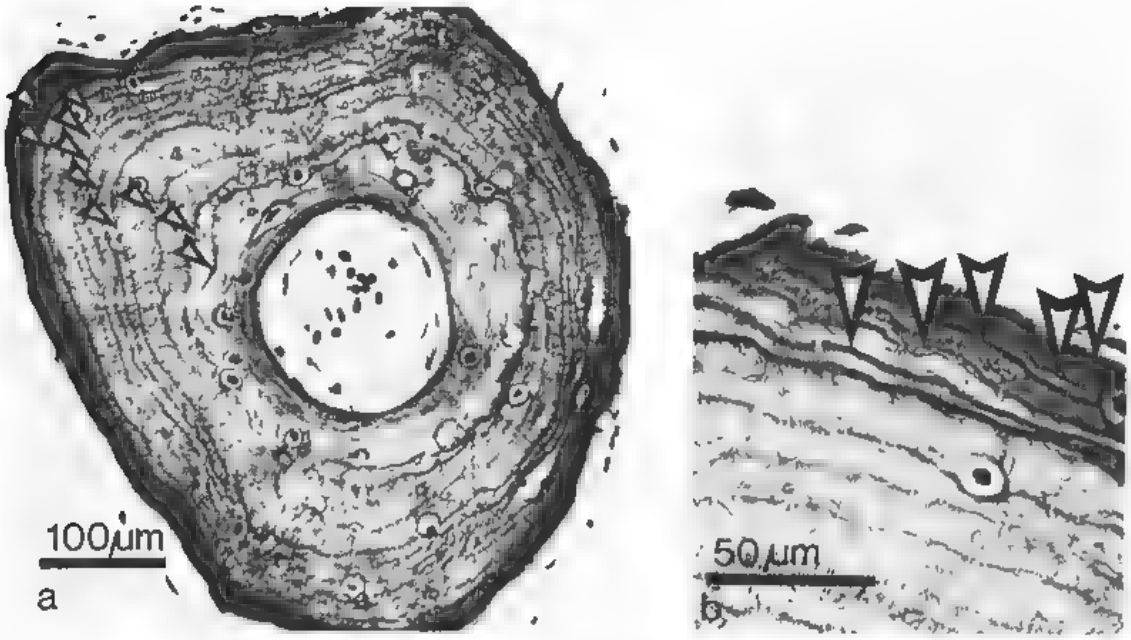

Fig. 1 – Cross section of the humerus of a 15 years old Alpine newt female. a: LAG formed during the first 10 years of life. b. LAG become narrow after the newt starts to reproduce Fig. 1b is taken from another cross section of the same bone shown in fig. 1a

population. During the summer period the percentage of marked animals in consecutive samples increased linearly with the total amount of newts marked in this year (SCHUHMACHER-ESCHMEYER plot; KREBS, 1989 35), showing that a constant population size was reached for a short time interval after migration into the lake.

RESULTS

No marked animals from Lake Dreibrüdersee were found in other breeding sites. Due to the isolated position of the lake and the high recapture rates of individually marked newts, any interchange with other populations seemed unlikely. There was no other breeding pond available in the vicinity of Lake Dreibrüdersee.

Both sexes started to breed late in life, first entering the breeding site at the age of 10 years. The long winter period resulted in clear lines of arrested bone growth (LAG), which were very close together after the animals had started to reproduce (fig. 1a). After 10 years age, bone growth was strongly reduced, resulting in a darkly staining outer zone of narrow LAG (fig. 1b). No animals younger than 10 years age were caught in the breeding sites indicating that the younger newts in this population lead an entirely terrestrial life.

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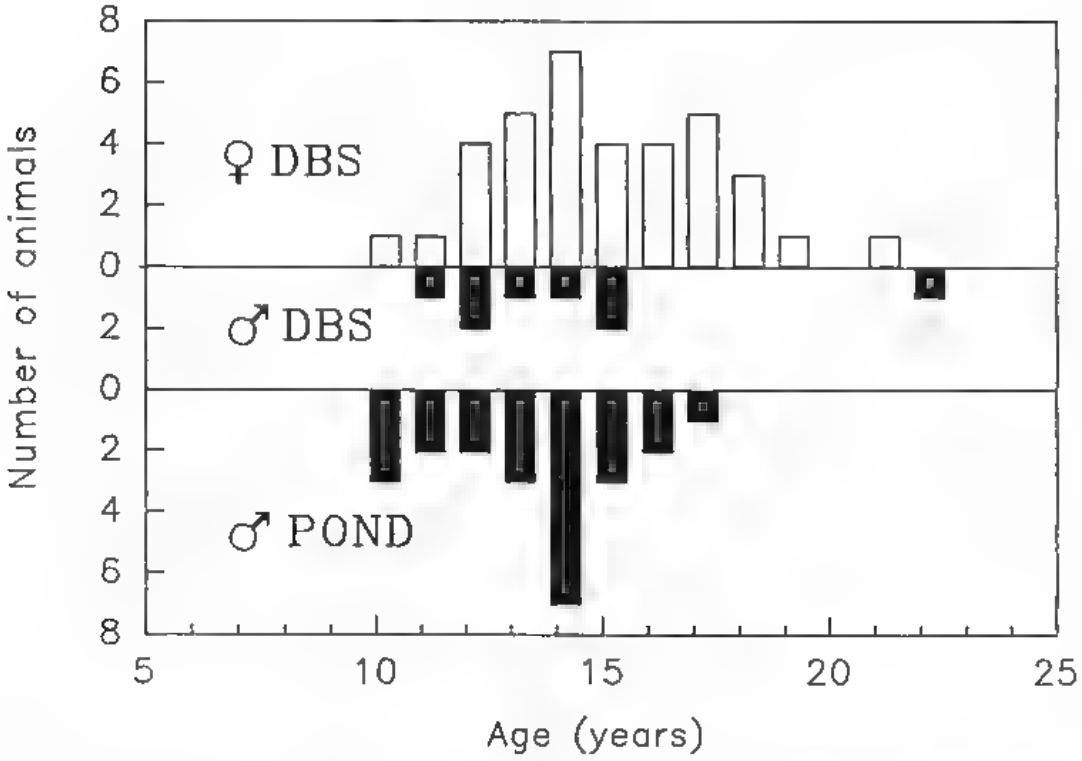

Fig 2. – Age structure of the breeding populations of Alpine newts from Lake Dreibrüdersee (DBS) and a nearby pond.

Animals 14 years old constituted the largest age class (fig. 2). Longevity exceeded 20 years in one female and one male newt from Lake Dreibrüdersee. The average annual survival rate derived from the age structure was estimated to be 0.67 ± 0.003 (Φ ± S.E.) for females from Lake Dreibrüdersee and 0.45 ± 0.012 for males from the pond, meaning that on average 67 % of the females and 45 % of the males survived from one year to the next.

Estimates of annual female survival rates (JOLLY-SEBER method) were above 0.70 (Table I) Approximately 60 % of the females (Φ ± S.E. = 0.609 ± 0.043) and 40 % of the males (Φ = 0.397 ± 0.087) present in 1986 survived to 1988. Assuming a constant probability of survival in this two-year interval yields annual survival rates of 0.78 and 0.63 for females and males, respectively. From 1988 to 1992, the sample size of males was too small for application of the JOLLY-SEBER model. The results indicate that males suffered from higher mortality than females.

The newt population in Lake Dreibrüdersee consisted of approximately 500-800 females and 150 males, resulting in a biased sex ratio of 1/3.7 to 1/4.8 males to females (Table I). Estimates of population size with different mark-recapture models were within the confidence limits of each other.

Source MNHN, Paris

Table I. - Population size, sex ratio and survival rate of Alpine newt adults in Lake Dreibrüdersee estimated with mark-recapture experiments. Sex ratio: ♂/♀. No animals were marked in 1987.

Year	Population size (N)		Survival rate $\Phi \pm$ S.E.
	PETERSEN [P] / SCHUHMACHER [S] (95 % C.L.)	JOLLY-SEBER N ± S.E.	
1986	♀: 773 (541-1314) [P]		1986-1988: ♀: 0 609 ± 0.043 ♂: 0.397 ± 0 087
1988	♀: 517 (466-580) [S] ♂: 149 (125-184) [S] Sex ratio: 1/3.5	546 ± 40	0.824 ± 0.053
1989	♀: 708 (609-845) [S] ♂: 156 (122-232) [P] Sex ratio: 1/4.6	807 ± 58	0.747 ± 0.090
1990	-	664 ± 86	0.965 ± 0.186
1991	♀: 682 (321-1443) [P]	596 ± 102	-

DISCUSSION

Alpine newts in temperate environments start to reproduce at three to four years of age and live for a maximum of 10 years (SMIRINA & ROČEK, 1976, SMIRINA & SUFIANIDU, 1985; MIAUD, 1990). The present study has shown that first reproduction can be significantly delayed due to cold temperature conditions. Adults have to use a very short summer period for reproduction. The average yearly ambient temperature at Lake Dreibrüdersee is around 2° C, resulting in slow growth rates. Growth is further reduced with the onset of first reproduction, as more energy has to be put into gonadal development. Strongly reduced bone growth after 10 years age and the fact that no younger animals were caught in the breeding sites indicate that Alpine newts cannot reproduce earlier in life under these environmental conditions

Animals from Lake Dreibrüdersee were bred under laboratory conditions simulating lowland temperature regimes. They reached body size of breeding animals within two to three years, showing that reduced growth was not genetically determined in this population (pers obs) Food availability was high in Lake Dreibrüdersee and reduced growth did not result from limited resources in the lake. During the second half of their aquatic period, individually marked females regained biomass lost during oviposition (pers. obs.).

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A long phase of hibernation followed by a comparatively short period of activity in summer probably did not support the development of double LAG reported for other *Triturus* populations (CAETANO et al., 1985; CAETANO & CASTANET, 1993).

The average female survival rate calculated with the ROBSON & CHAPMAN formula is close to the estimate of 0.65 published by MIAUD (1991) for a lowland Alpine newt population in south-east France. Nevertheless, mark-recapture experiments yielded higher survival rates above 0.7 (Table I). This difference resulted from not including age classes 10 to 13 in the calculation of survival rate with the ROBSON & CHAPMAN formula. Some of the 10 to 13 years old specimens did not enter the breeding sites. Additionally, the age of animals older than 15 years may have been underestimated, because LAG became increasingly more difficult to distinguish. For this reason mark-recapture experiments gave a more realistic description of survival.

Males seemed to have a higher mortality rate than females. These different survival rates in males and females clearly need to be investigated further. In their detailed studies of Alpine newts at similar altitudes in the Austrian Alps, FABER (1991) and GUTLEB (1990) also found skewed sex ratios of 1/1 45 and 1/1 22 males to females respectively. Higher mortality during the spring migration could be the reason for the lower survival rates in adult males. Adult males started spring migration before the females. This was also found for other newt species (BLAB, 1978; HARRISON et al., 1983; GRIFFITHS, 1984). During migration at the beginning of June, temperature often drops below freezing At this time males enter numerous small water bodies on their way to the breeding site. These puddles easily freeze and the newts suffocate. Of 50 dead newts collected in the spring 48 were males.

RÉSUMÉ

L'âge individuel de 67 Tritons alpestres d'un plateau karstique des Alpes calcaires du nord-est de l'Autriche (Totes Gebirge, altitude 1650 m) a été mis en évidence par squelettochronologie s'appuyant sur des coupes transversales d'humérus. En raison de la longue période d'hiver, les animaux des deux sexes commencent à se reproduire à l'âge de 10 ans L'espérance de vie s'élève à 20 ans, l'animal le plus vieux observé ayant atteint l'âge de 22 ans Le taux de survie, estimé en fonction de la structure d'âge de la population et d'expériences de marquage-recapture, semble plus bas chez les mâles, ce qui entraîne un biais du sex-ratio en faveur des femelles Ce phénomène pourrait être dû à une mortalité élevée des mâles pendant la migration de printemps.

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Meetings

SIXTH MEETING OF THE *TRITURUS* GROUP

Schloß Ulmerfeld, 120 km west of Vienna, Austria.
9-12 September 1994.
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WORKSHOP ON POPULATION BIOLOGY OF AMPHIBIANS

Vienna, Austria.
14-17 September 1994.
For information please contact:
Dr. Walter HÖDL or Dr. Günter GOLLMANN, Institut für Zoologie der Universität Wien, Althanstraße 14, 1090 Wien, Austria.
Fax: +431 31336 700.

SECOND INTERNATIONAL SYMPOSIUM ON ECOLOGY AND GENETICS OF EUROPEAN WATER FROGS

Wrocław, Poland.
19-25 September 1994.
For information please contact:
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SECOND INTERNATIONAL ASIAN HERPETOLOGICAL MEETING

Ashgabat, Turkmenistan.
25-30 August 1995.
For information please contact:
- Dr. Sakhat M. SHAMMAKOV, Institute of Zoology, Academy of Sciences of Turkmenistan, Azady Street 59, 744000 Ashgabat, Turkmenistan.
- Dr. Theodore J. PAPENFUSS, Museum of Vertebrate Zoology, University of California, Berkeley, California 94720, U.S.A.
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